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SOME ATTEMPTS TOWARD EXPERIMENTAL ZOOGEOGRAPHY[1]

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During my stay in the United States in the spring of 1951, it was suggested that I should give, for the information of American students, a brief summary of the methods and conclusions of what might be called experimental zoogeography, mostly from the third part of my book (Lindroth 1949) on the carabid beetles of Fennoscandia (Finland and Scandinavia with small adjacent areas). This book was written in German, with an extensive English summary, but published in a journal not widely distributed in America. The following abstracts refer mainly to the experimental parts of the work which are of more general application.

METHODS

The purpose of the experiments was to isolate external factors (temperature, moisture, light) which apparently control the distribution of certain Fennoscandian carabids in nature, and to study the reactions of the animals to them. Primarily, the *preferences* of different species were investigated by means of different experimental gradient apparatuses ("orgels"). The "temperature-orgel" was the simple type first used by Herter (1924). The "substratum-orgel" (Fig. 1) used to study reactions to hygric and chemical factors was invented by Krogerus (1939). The "universal orgel" (Figs. 2, 3) is new. It is a linear or a circular apparatus in which insects were exposed to the simultaneous influences of two or three factors in different combinations. In many cases the tolerance to extreme temperatures and desiccation was studied as well as the insects' preferences. It should be emphasized that the numerical results of the experiments are not absolute partly because of uncontrolled secondary factors, but mainly because different individuals of one species or even the same individuals in different situations often show different reactions, and of course different species often react differently too. I have tried to average out minor errors by making the same experiment simultaneously or under as nearly as possible identical circumstances with several individuals of a species, or with more than one species. Thus it was possible to obtain significant *comparative* figures on, for example, the thermal preferences of a series of taxonomically and ecologically related species. Of course the apparatuses and techniques here described are applicable to many other groups of animals besides insects.

The first two groups of experiments concern questions of general ecological and zoogeographical importance.

[1] Professor Lindroth put this paper together partly at my suggestion, and at his request I have edited it. The purpose of the paper is not to describe experiments in full, but to make known to Americans that the experiments have been done and what the results have been. The original accounts of the experiments should be consulted by interested persons. The work here summarized is an example of what can be done when a first-class taxonomist, which Professor Lindroth is, turns his hand to experimental ecology and zoogeography.

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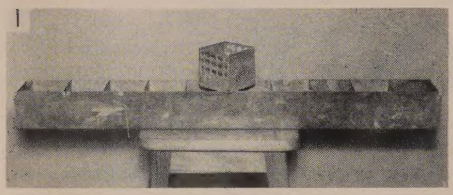


FIG. 1. Substratum-orgel (Krogerus' model), consisting of a long zinc box (80 x 8 x 8 cm) containing a series of small zinc boxes (7.5-cm cubes) with their walls perforated so that beetles can move freely from one box to another. The cover is of fine-mesh screen. In experiments the small boxes are filled with substratum materials varying in one factor, and the distribution of beetles placed in the apparatus is determined, in relation to the factor concerned, after one or 2 days. See Lindroth (1949, pp. 73 ff.) for further description.

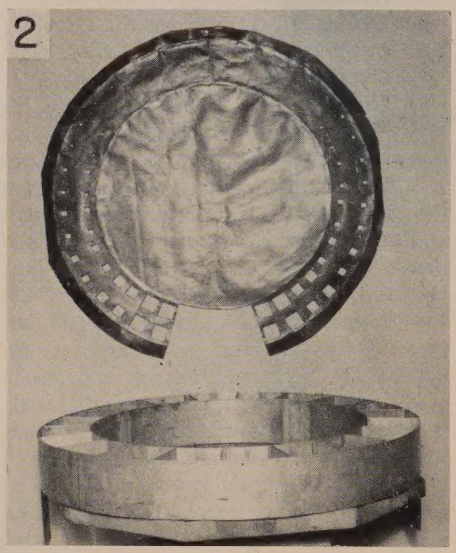


FIG. 2. Circular universal-orgel, with black cover used in experiments in which light was a factor. This is a modified substratum-orgel for determining the simultaneous effects of 2 or 3 factors in different combinations, *e.g.* variation in the substratum, temperature (controlled through copper plates attached to the ends of the apparatus), and light. See Lindroth (*op. cit.*, pp. 85 ff.) for further details.

1. Stable and Labile Preferences

This subject was briefly treated in an earlier paper (Lindroth 1943). It was studied for several species. Stable preferences are exemplified by *Pterostichus anthracinus* Illiger, in which a field population (P-generation) showed exactly the same thermal preferences as an F_1-generation from the same stock bred under constant indoor temperature. A good example of a labile preference is the reaction of *Harpalus punctatulus* Duftschmid to moisture in different summer months (Fig. 4).

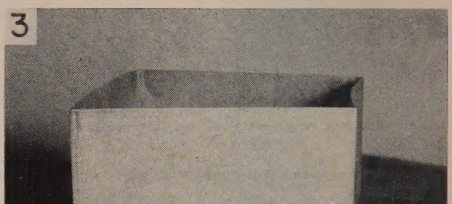


FIG. 3. Box for the circular universal-orgel. The sides of the box are not perforated but have slits 5 mm wide 5 mm from the bottom which allow beetles to pass but leave the air mass of the box relatively isolated from adjacent boxes.

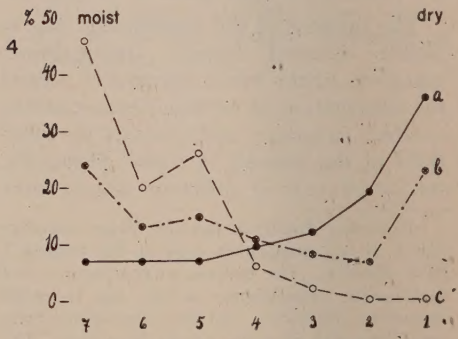


FIG. 4. Distribution of *Harpalus punctatulus* Duftschimdt in relation to moisture in a substratum-orgel of 7 compartments: a) in May, b) in June, and c) in July after 2 days in moisture-saturated air. Horizontal coordinates represent the 7 compartments or the orgel from moist to dry. Vertical coordinates show percentages of individuals of each lot of beetles in each compartment.

2. Near Identity of Ecological Requirements

Brachynus crepitans Linnaeus and *Agonum dorsale* Pontoppidan regularly occur together but are not dependent on each other. They represent the rare case of two species with nearly identical ecological demands. It might be expected that a comparison of the reactions of these two taxonomically very different species would reveal similar preferences and tolerances of great ecological and geographical importance. This proved to be so as regards cold tolerance and moisture preference. The thermal preferences of the two species (Fig. 5) were quite different, however. The results of these experiments should be applicable to other more or less xerophilous carabids in northern areas.

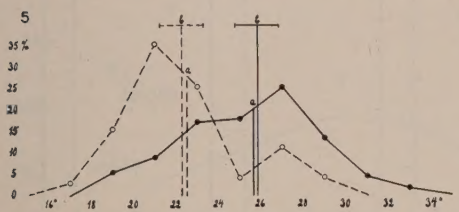


Fig. 5. Distribution of *Brachynus crepitans* Linnaeus (solid line) and *Agonum dorsale* Pontoppidan (broken line) in relation to temperature in a temperature-orgel. Horizontal coordinates are temperature (Centigrade). Vertical coordinates are percentages of individuals in the compartments of the orgel. Arithmetic mean (a) and statistical mean (b) are shown for each species by vertical lines, and the expected errors of the statistical mean are indicated by horizontal lines.

3. The "Limestone Species"

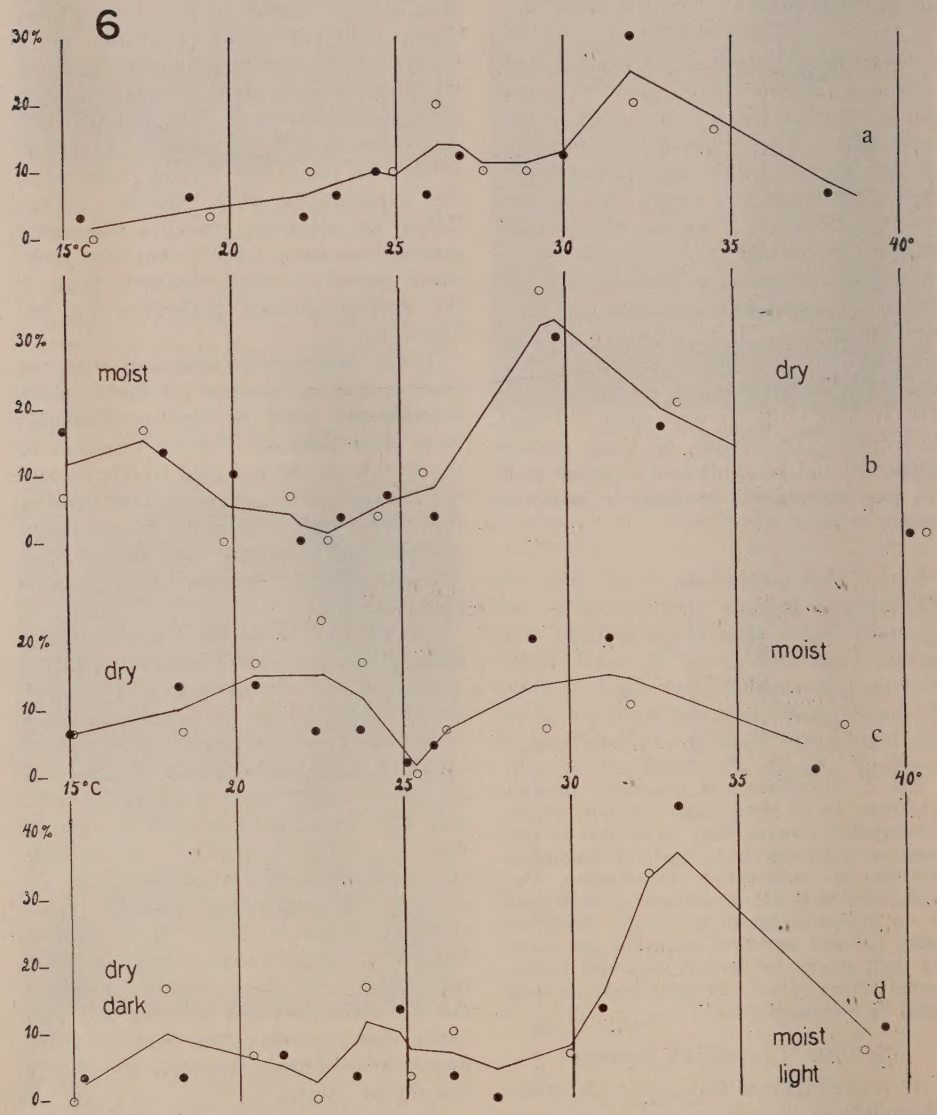
It is well-known that many plants are dependent on limestone, and so are various insects in Fennoscandia. They are usually termed calciphilous. Examples are some members of the carabid genus *Harpalus*. So a series of fifteen species of *Harpalus* was selected for experimental investigation of the "limestone-species."

In the "substratum-orgel," all species tested seemed insensible to different proportions of $CaCO_3$, even when it was dissolved in water saturated with CO_2. Nor did the species in question seem to react to the pH of the substratum. In a series of experiments made to find whether the "calciphilous" carabids could distinguish limestone gravel from siliceous gravel, five species of *Harpalus* seemed to prefer the former. But when the experiments were repeated, substituting for siliceous gravel a clay-schist gravel free from $CaCO_3$ but like limestone gravel in other qualities, none of the species showed preference for the limestone.

These experiments indicated that the confinement to limestone of the carabids investigated must be due to demands other than chemical. So the reactions of the insects to thermal and hygric factors were tested in the usual manner, and it was found that in general the supposed "calciphilous" Harpali are (in Fennoscandia) strongly thermophilous or xerophilous or both.

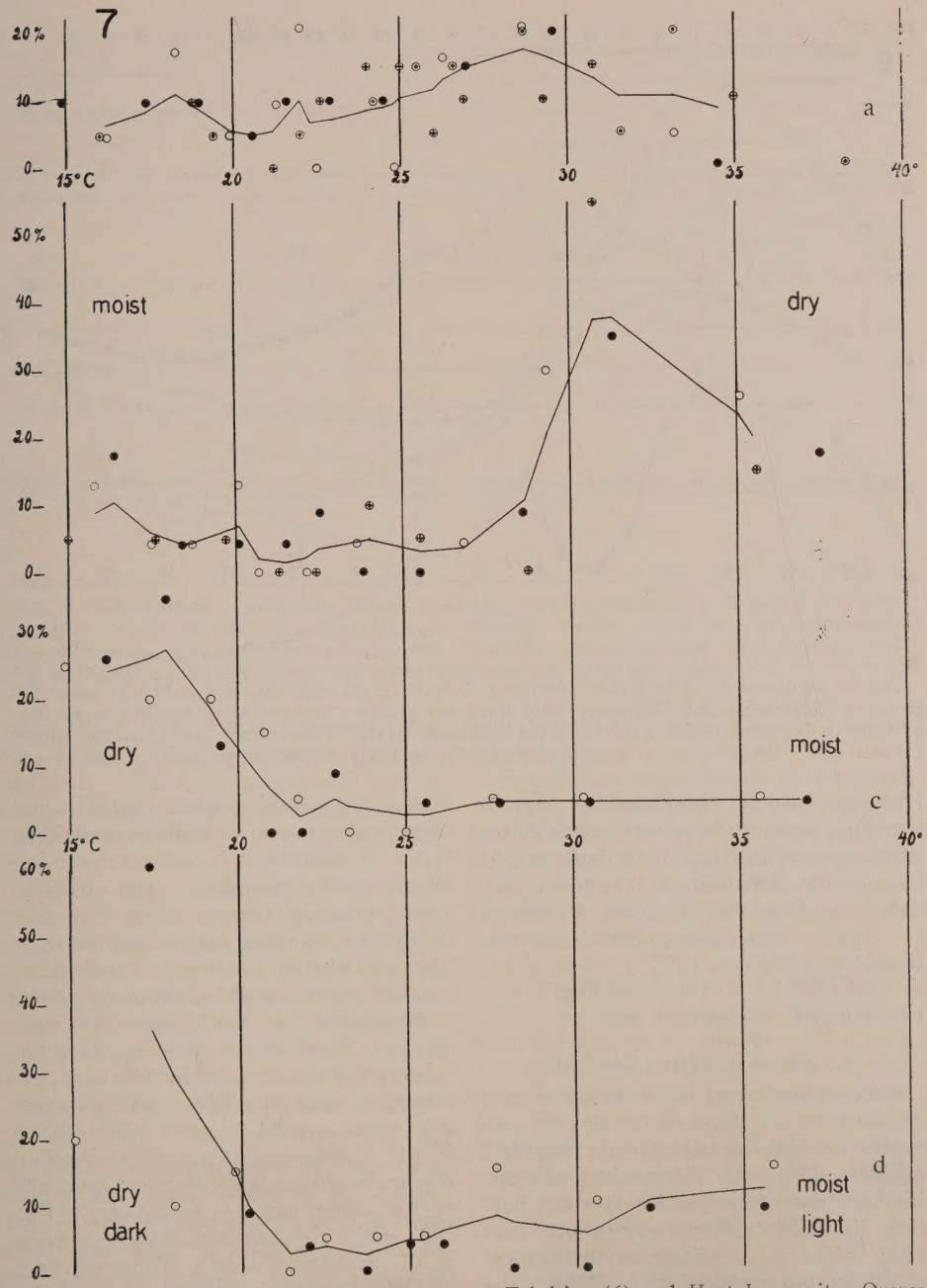
An attempt to decide what factor in each species plays the important role was made through experiments in the "universal orgel," where the relative strength of reactions to simultaneous thermal and hygric factors was studied. Among the eleven *Harpalus* species tested in this way, the thermic preference of *H. azureus* Fabricius (Fig. 6)and the hygric preference of *H. serripes* Quensel (Fig. 7) proved to be particularly strong. (Contrary behaviour is shown by *H. aeneus* Fabricius (*viridiaeneus* Beauvois), the most ubiquitous species tested, of which the thermal preference is weak and also easily disturbed by other factors. This may be true of other eurytopic and widely distributed species.)

The thermal qualities of both rock and gravel of Fennoscandian Cambro-Silurian limestone were compared with those of granite by means of laboratory measurements on small quantities (Fig. 8). All reactions proved to be more rapid in granite, which therefore had the highest daily maxima and the lowest minima. This difference was found to be even greater in field measurements on each side of a fault fissure (Cambro-Silurian



limestone *contra* granite) at Rättvik in Dalecarlia (Fig. 9). So it seems the Cambro-Silurian limestone alters the microclimate in an oceanic direction, that is, it tends to prevent extremes of both heat and cold. Especially by preventing extremes of cold and by tempering the winter climate, the limestone must have a great influence on distribution of life. Its effect is to lengthen the annual period of activity of ground-living insects and to permit the latter to occur farther north than they otherwise could do. On the island of Gotland in the Baltic, the effect of a limestone substratum is to lengthen the annual period of activity of ground-living insects an average of about three weeks.

Archaic limestone, *e.g.* marble, or limestone occurring as moraine only (both



FIGS. 6 AND 7. Distribution of *Harpalus azureus* Fabricius (6) and *Harpalus serripes* Quensel (7) in relation to temperature (Centigrade), moisture, and light in the universal-orgel, with a) temperature the only variable, b) temperature and moisture "cooperating" (temperature and dryness increasing together), c) temperature and moisture "competing" (temperature and moisture increasing together), and d) temperature "competing" with moisture and light (temperature, moisture, and light increasing together). Horizontal coordinates show temperature (Centigrade) and varying degrees of moisture and (at bottom) light. Vertical coordinates show percentages of individuals in compartments of the orgel.

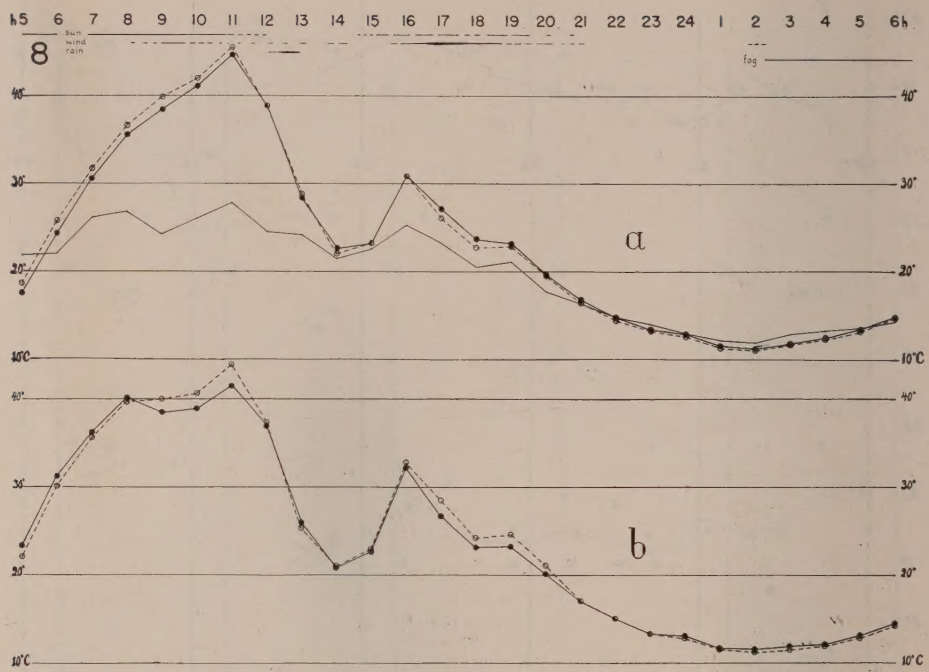


FIG. 8. Temperature (Centigrade) during a 25-hour period beginning at 5 A.M.: a) under flat pieces of Cambro-Silurian limestone (solid line) and granite (broken line) (fine line is air temperature during same period), and b) in dry limestone gravel (solid line) and siliceous gravel (broken line). Distribution of sunshine, wind, rain, and fog during the period is shown at top.

types are widely distributed in Fennoscandia), seems to have no positive effect on the ground fauna, as it no doubt would have if the influence of limestone were chemical. One feels inclined, therefore, to regard the "petrophilous" insects, treated by Holdhaus (1911) for the Alps, as controlled by thermal and hygric factors rather than chemical ones.

4. Other Edaphic Factors

Some experiments were carried out to demonstrate the dependence of some carabids on the mechanical and chemical qualities of the soil. The mechanical qualities are determined mainly by the particle dimensions. Many species with digging habits are sensitive to this factor, avoiding too coarse sand. This was clearly manifested by species of *Harpalus* and *Dyschirius* in the "substratum-orgel."

As to chemical properties of the soil, it has long been well known that certain insects, including several carabids, are more or less bound to biotopes containing NaCl. A distinction is made between halobiont (salt-demanding) and halophil (salt-preferring) forms. Only five true halobiont carabids occur in Fennoscandia. The undetermined number of "halophils" includes species confined to sandy shores (independent of NaCl) and two species of *Bembidion* (*aeneum* Germar, *minimum* Fabricius) which, through experiments in a modified "substratum-orgel," were proved to react positively to NaCl. *B. aeneum* has an inland distribution in Scandinavia conforming very well to the occurrence of Yoldia-clay (Fig. 10), which is supposed still to contain small quantities of NaCl. These two species of *Bembidion* probably are real halobionts, but they demand only small amounts of salt. It is a question whether the term "halophil" is worth using. It implies that certain species "love" NaCl

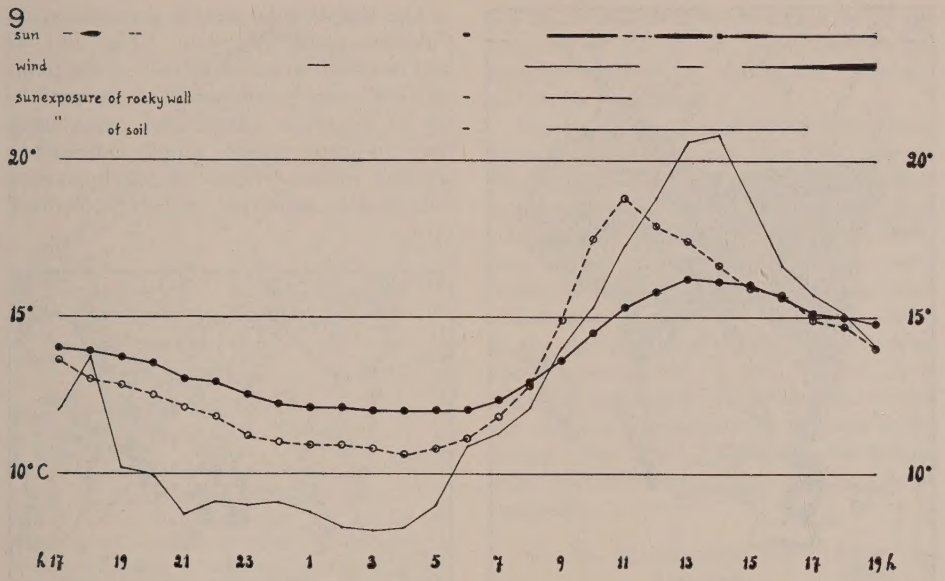


FIG. 9. Temperature (Centigrade) during a 26-hour period (beginning at 17 hours, or 5 P.M., June 4th) on opposite sides of a fault fissure at Rättvik, Sweden: solid line, on orthoceratite-limestone 5-6 cm. deep; broken line, on granite. Fine line is air temperature. Distribution of sunshine and wind, and of exposure to sun of the rock and soil, is shown at top.

rather than other factors characterizing the seashore. This is not known to be so, and it is difficult to understand how it can be so unless the species actually demand NaCl at least in very small quantities.

It is not easy to demonstrate an actual demand for other chemicals among Carabidae. It has been supposed that some species which are more or less characteristic of cultivated land might be favoured by artificial fertilizer and that this might explain their rapid spread in recent years. *Amara ingenua* Duftschmid was chosen and tested as a possible example of this, and *A. praetermissa* Sahlberg, which rather avoids cultivated land, was used as a control. Neither of the species showed any positive reaction to the commonly used sorts of artificial fertilizer in the "substratum-orgel." But when tested with the fruits and seeds of several common weeds, *A. ingenua* showed a clear preference for the fruits of *Polygonum aviculare*. This *Amara* may be secondarily favoured by fertilizers which favour this weed.

Unpublished experiments by Krogerus (*cf.* also Krogerus 1939) have shown that certain "stenionic" insects confined to peat-bogs react positively to a substratum with low pH value. But most carabids, including hygrophil species, are indifferent in this respect.

5. Species with Wing Dimorphism

No less than 50 of the 362 Fenno-scandian species of carabid beetles have dimorphic wings. The wing dimorphism is not sexual and has an hereditary basis. The brachypterous wing is a dominant (Lindroth 1946), and consequently the macropterous individuals, which usually can fly, are homozygous and cannot produce brachypterous offspring, unless by recurrent mutation.

Darlington (1943) has suggested that the brachypterous individuals of dimorphic carabids may be generally favoured owing to their "higher viability" (an idea supported by the breeding results of Jack-

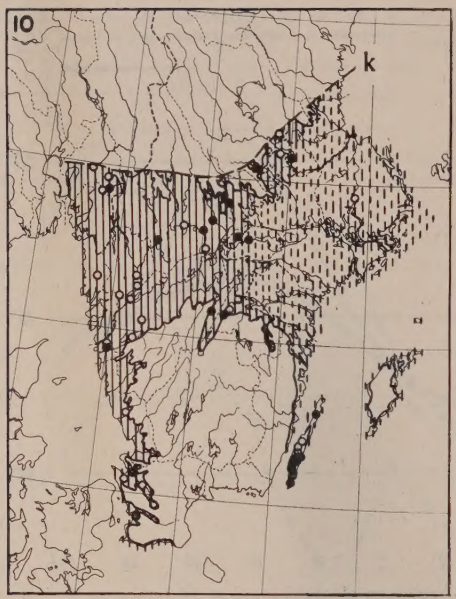


FIG. 10. Inland records of *Bembidion aeneum* Germar in Scandinavia, showing virtual restriction to slightly saline soil. Parts of the land south of the ice-border (k) which then existed which were covered by the Yoldia Sea are indicated by vertical lines, which are interrupted in the area later covered by (and leached by) the Ancylus Lake. Collections of more than one specimen are indicated in solid black; of single specimens, by open circles.

son, 1928, with *Sitona*). In order to test this a series of experiments on the preferences and tolerances of brachypterous and macropterous individuals of the same species was made. No general "higher viability" of the brachypterous forms was found. The material used was limited, but the experiments make it unjustifiable to ascribe *a priori* a higher selective value to the brachypterous than to the macropterous forms of dimorphic carabid species. This being so, the unequal distribution of long- and short-winged forms within the range of a species, if pronounced, is to be accounted for by the different powers of dispersal alone. Although they are not not founded on actual experiment, it seems appropriate to mention here the conclusions which can be drawn from "dimorphic maps" and to illustrate them with a few examples.

The simple rule, clearly exemplified by *Calathus mollis* Marsham (Fig. 11), is that macropterous individuals—"the parachutists"—are predominant at the periphery of a species range, and presumably they indicate recent range extensions; while a preponderance of brachypterous individuals indicates a long-colonized area.

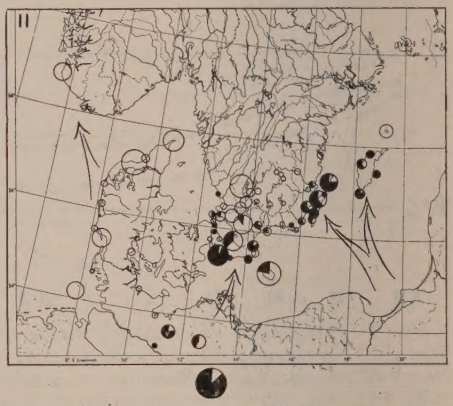


FIG. 11. Distribution of wing-forms of the dimorphically winged *Calathus mollis* Marsham: black circles and sectors indicate brachypterous individuals which cannot fly; open circles and sectors, macropterous individuals some or all of which can fly. The area of the circles is proportional to the number of individuals in each lot examined. The pattern of distribution reflects spread northwards and northwestwards by flight.

Calathus erratus Sahlberg (Fig. 12) is of special interest because it shows that, along the coast of western Norway, selection does not work in favour of the brachypterous form.

A different picture is given by *Bembidion grapei* Gyllenhal (*nitens* Leconte) (Fig. 13). Its distribution as a whole, without regard to wing-state, would suggest that the species is a postglacial immigrant into Fennoscandia from the east, but the occurrence of brachypterous individuals tells the contrary. It doubtless survived the last glaciation (Würm) in western Norway.

During a glacial age small, isolated, coastal refuges form islands for life where selection is presumably strong in favour

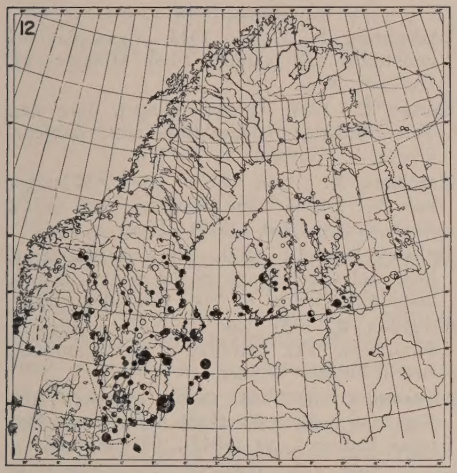


FIG. 12. Distribution of wing-forms of *Calathus erratus* Sahlberg. See Fig. 11 for explanation of symbols. The main watershed of southern Norway is indicated by heavy broken line. This pattern of distribution too reflects spread northwards.

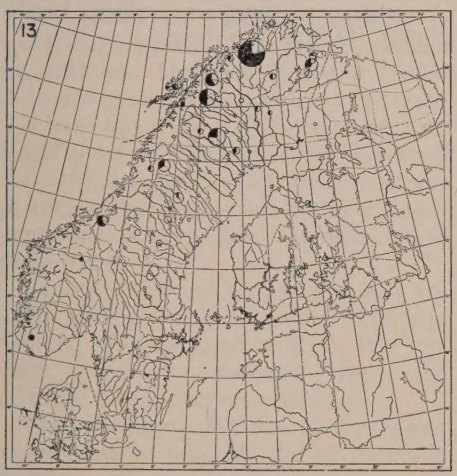


FIG. 13. Distribution of wing-forms of *Bembidion grapei* Gyllenhal. See Fig. 11 for explanation of symbols. The supposed Würm glacial refuges are indicated by broken lines. This pattern of distribution reflects spread of winged individuals away from the refuges.

of flightless insects. During the initial and final phases of every glacial age, on the other hand, the enormous and in part rapid changes of habitats are in favour of flying insects. So, in repeatedly glaciated areas, wing-dimorphism must itself be a considerable advantage to an insect, for it allows the population to be rapidly adapted to alternately unstable and stable conditions.

Among the dimorphic carabid species of Fennoscandia, at least nine may be regarded as "winterers" within the limits of Fennoscandia during the "Würm" glaciation. The present distribution of these nine species shows that, of them, only *Notiophilus aquaticus* Linnaeus is capable of living in "high-arctic" conditions. Five of the species have never been recorded above forest limit at all. These facts strongly contradict prevalent ideas about the climatic conditions in Fennoscandia during the last glaciation—conditions were probably less severe than has been supposed.

6. An Experiment on Flight Direction

The indisputable fact that dispersal of insects in the Baltic area has taken place more from the east than from the west suggested investigation by means of a special apparatus (Fig. 14) of the influence of the sun on flight-direction. It was found that at least some carabids usually swarmed and flew in the evening and tended to start their flight *toward the setting sun,* so that they flew mainly from east to west (Fig. 15). However, it

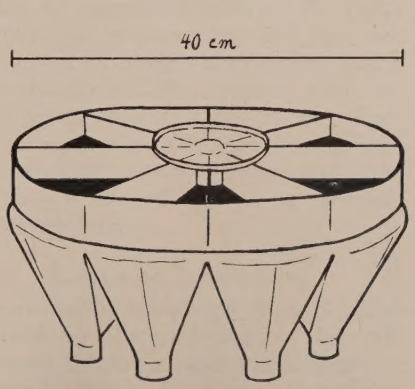


FIG. 14. Flight-direction apparatus. In use it was covered with a dome-shaped top of transparent celluloid. Insects were placed on the flat dish at middle and, after flight, were recovered under the funnels.

would be premature to suppose that this is an important factor in the distribution of insects in general.

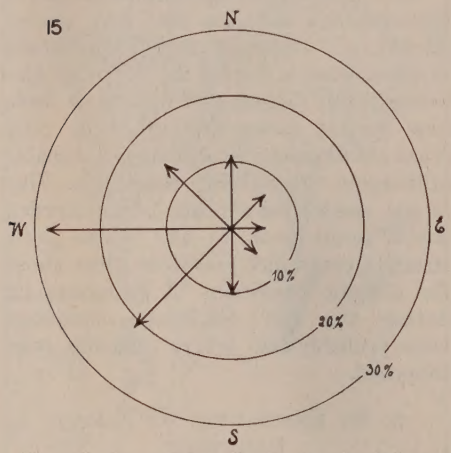


FIG. 15. Percentage distribution in different directions of 100 individuals of *Oodes gracilis* Villa started in the flight-direction apparatus between 5 and 7 P.M. in bright sunshine.

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EFFECT OF ENVIRONMENTAL CONDITIONS ON SURVIVAL AND GROWTH OF FOREST TREE SEEDLINGS UNDER FIELD CONDITIONS IN THE PIEDMONT REGION OF NORTH CAROLINA

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INTRODUCTION

One of the most troublesome problems confronting the forester is the establishment of natural stands of desirable timber species. Frequently the course of natural forest succession interferes with establishment of preferred species and density of reproduction. This problem is especially pressing in the Piedmont Plateau region of North Carolina. Because of their rapid growth and the desirable qualities of their lumber, both loblolly and shortleaf pines are preferred species. Neither, however, is a dominant member of the climax vegetation for this area and consequently under natural conditions pure stands of these species are gradually replaced by species of a climax forest type dominated by oaks and hickories (Oosting 1942). As more and more of the pine areas reach maturity following abandonment of farm lands and fires, the problem of arresting the natural successional pattern and perpetuating the desires species in a dominant position in the forest assumes larger proportions.

Several solutions to this problem are open. The pines may be, and often are, planted. However, in general, the forester prefers to maintain the forest through natural regeneration.

The silvicultural systems in use by foresters serve to influence the environment in such a way as to aid natural regeneration. However, it is often not clear as to just how environmental factors have been altered by a given silvicultural system. For example, any particular cutting system will alter the light, soil moisture, and temperature conditions within a stand, to mention just a few of the factors which are changed. Much confusion has arisen from the failure to realize the complex nature of the environment of a forest stand and the many changes in this environment which accompany cutting systems.

The present experiment was designed to clarify the relative and absolute effect of factors affecting survival and growth and thus to help provide a sound basis for silvicultural practice. Light, soil moisture, and soil texture were selected as environmental factors to be studied in the field and to a certain extent controlled so as to cover the full range of conditions over which these factors normally vary in the lower Piedmont Plateau. It is known that seedlings respond to extremes of light and soil moisture. The problem was to determine the responses under the normal range of conditions in the field. The plans called for measuring the environmental conditions, making concomitant measurements of the survival and growth of seedlings of selected species, and then determining by regression analyses the exact relationships between the seedlings and the factors of their environment which were measured. The species were selected from several stages of the vegetational succession to obtain the reactions of species from totally different ecological positions to the same sets of environmental conditions.

REVIEW OF LITERATURE

A reasonable knowledge of the physical requirements of trees is basic to their silvicultural treatment and consequently a number of studies have been undertaken to determine the effect of certain environmental factors on their survival, growth, and development. This study was re-

[1]The author wishes to express his gratitude to Prof. T. S. Coile for suggesting this problem and to Prof. F. X. Schumacher for much assistance with the statistical work.

stricted to one year old seedlings, so only that literature pertaining to the behavior of young seedlings will be reviewed.

There has been a sharp difference of opinion among workers as to the most important factor in survival and growth in the field. Broadly, there are two groups, those who believe that light is the most important determinant and those who ascribe the leading role to soil moisture.

A number of experimenters have dealt with the light variable alone and in combination with other factors. Pearson (1929, 1930) conducted field experiments to determine the relative effect of light and soil moisture on survival and growth of important species in the Southwest. He concluded that increasing soil moisture was ineffective in promoting survival in quantity and that at low light intensities all species were weak and would not survive in large numbers. Shirley (1929) found that loblolly pine seedlings gained steadily in weight with increasing light intensities, the gain being in direct proportion up to 40 per cent of full light. The seedlings of this species could survive for six months at very low light intensities but were unable to add any weight. In a study with Norway pine seedlings, Shirley (1932) concluded that 35 per cent of full sunlight was sufficient to allow satisfactory establishment, but light below 17 per cent resulted in uncertain establishment. In a very comprehensive study of a number of coniferous species, Shirley (1945) investigated the effect of both light and soil moisture under nursery and field conditions. In the nursery, with adequate soil moisture, survial of all species was uniform down to 43 per cent of full sunlight but decreased below that figure. Seedling weight increased up to 43 per cent of full sunlight for some species while others continued to increase in weight up to 100 per cent of full sunlight. In the field, increasing soil moisture by trenching greatly aided survival. His results showed that 13 per cent of full sunlight was inadequate for survival while 20 per cent was adequate. In contrasting these figures with the considerably lower figures reported by some other workers (Bates and Roeser 1928 and Grasovsky 1929), he pointed out that their figures were obtained with all other factors controlled and favorable for growth. His conclusions were that under natural conditions in the Lake States, seedling survival was more dependent upon adequate light intensity than on any other factor.

Haig (1936) in a complete field and nursery study of western white pine established that a 5 per cent radiation intensity was sufficient to allow seedlings to survive the first season. However, the seedlings added little weight under such conditions. The response to light was quite different among species. Douglas fir, western larch, and grand fir all gave heaviest plants in part shade, whereas western white pine showed greatest weight increase in full sunlight. Similar results have been reported from the northeastern states by Moore (1926) and Smith (1940). They concluded from studies of coniferous seedlings that light was the most important factor for survival and growth. Moore reported that he was unable to counteract the shade effect by adding water artificially to shade grown seedlings.

In order to establish the exact response of seedlings to variation in light intensity, several experiments have been conducted under controlled laboratory conditions. Mitchell (1936) working on eastern white pine found a steady progression in weight up to and including 100 per cent of full sunlight. Baker (1945) had similar results with variation in light intensities but found that the shapes and slopes of the growth curves varied with the species. Bates and Roeser (1928) grew coniferous seedlings with light intensities as low as 0.7 per cent of full sunlight when other conditions were favorable. However, they pointed out that such seedlings would probably not survive when other environmental factors were unfavorable. To determine if minimum light requirements could be modified by increasing

available nutrients, Steinbauer (1932) grew red ash seedlings in nutrient solutions of varying concentrations near the minimum light requirements. He found that the minimum light requirements could not be lowered by such means. Grasovsky (1929) concluded from laboratory experiments that the minimum light value for survival of several pine species was 3 per cent of full sunlight. From a comparison of this figure with field light measurements he concluded that light was not limiting in New England forests. Contrary to his interpretation it seems well demonstrated that light is often limiting under conditions of competition in the field.

A number of soil moisture studies have been carried on to determine the effect of this variable on seedling establishment. The early work of Fricke (1904) called attention to soil moisture. Fricke's work was expanded in the northeastern states by Toumey and Kienholz (1931). They compared trenched and untrenched plots under a forest canopy through which only 7 per cent of full sunlight was penetrating. During drought, they found that the surface soil in the trenched plots contained 2 to 9 times as much moisture as did surface soil in the untrenched plots. Eight years after establishment they reported more and larger seedlings in the trenched than in the untrenched plots. Reexamining these plots eighteen years after establishment, Lutz (1945) found that all of the white pine had died although the hemlock was doing quite well. He concluded that there was not enough light for the pine. However, the plots had not been retrenched in the meanwhile and soil moisture must have been progressively reduced over the years with the invasion of roots from the outside. Since soil moisture was decreasing and light was presumably constant, one might more logically conclude, in the absence of complete information, that the combination of low light intensity and reduced soil moisture was not sufficient for the pine.

Korstian and Coile (1938) established similar trenching experiments in the Duke Forest. Light intensities in the stands were from 3 to 84 per cent of full sunlight. Trenching resulted in an increase in the number of individuals, an increase in the number of species, and a greater luxuriance of growth. However, where the light level was only 3 per cent of full sunlight, the effect of trenching was considerably reduced. At a later date, Oosting and Kramer (1946) reported that many of the pines which had survived in the Duke Forest plots during the early treatment and observations were then dead and those remaining were spindly and unthrifty. However, again the soil moisture in the plots must have been very little different from that in the undisturbed forest since they had not been retrenched for a number of years.

The ecological relations of the tree species important in the Piedmont Plateau have received considerable attention. Coile (1940) conducting an intensive study of some species in relation to loblolly pine succession, pointed out that as the successional trend proceeds, the seedlings receive less soil moisture and as a result fail to develop adequately. He found that the oaks develop deeper, larger root systems than loblolly pine and thus can survive droughts better than pine. This relationship was also demonstrated in shortleaf pine succession by Billings (1938). Kozlowski (1949) studied these same species under controlled laboratory conditions. With 33 per cent of full sunlight both pine and oak were smaller in size as compared with plants grown in full sunlight. Furthermore, he found that the pine was reduced in weight more than the oak on a percentage basis. He was able to increase the weight of the shaded seedlings by increasing soil moisture.

It is obviously difficult to draw any clearcut conclusions from all of the work cited. For one thing, it is impossible to compare results obtained under different conditions. As an example, full sunlight is certainly not the same in some parts of the New England states as it is in the Piedmont Plateau. Another complication comes from the number of species studied.

The effects of light and soil moisture on one species may not be the same as on another otherwise similar species. Furthermore, not all of the environmental factors were controlled or measured in many of the studies, and this could account for many discrepances in results. It is impossible to conclude from the work reviewed whether light or soil moisture is the dominant factor in survival and growth of seedlings. It is doubtful if any such statement can be made for all forest tree seedlings since it probably varies with the species. It is clear from these experiments that no unqualified statements as to whether any one factor is limiting are justified. When dealing with an environmental complex, all of the major factors must be considered before one can arrive at any conclusions as to their effect on survival and growth.

Description of General Area

The present study was carried on in the Durham and New Hope Creek divisions of the Duke Forest in the vicinity of Durham, North Carolina. This forest, with its climate, physiography, and vegetation, has been thoroughly described elsewhere (Korstian and Maughan 1935) and need not be described in detail here. It is located in the gently rolling lower Piedmont region at an altitude of approximately 500 feet, with a considerable number of forest types occurring on the area. The climate is mild, with uniform precipitation distributed throughout the year and a two hundred day growing season. A great diversity of soil types and a number of soil parent materials occur on the area. The annual precipitation in inches is a matter of special importance for this experiment and will be considered in more detail later in the paper.

Methods

The species selected for the present study were loblolly pine (*Pinus taeda* L.), shortleaf pine (*Pinus echinata* Mill.), white oak (*Quercus alba* L.), southern red oak (*Quercus rubra* L.), red gum (*Liquidambar styraciflua* L.), and dogwood (*Cornus florida* L.). They were selected because of their diverse places in the successional trend in the Piedmont. The placement of these species in the succession in the Piedmont is given in Oosting's excellent paper (1942). Neither loblolly nor shortleaf pine are members of the climax forest although both form large and economically important stands which are part of secondary communities in the Piedmont. White and southern red oaks are both common members of upland and lowland climax communities. Red gum is important as an intermediate (in an ecological sense) in secondary lowland communities. It may be found in a great variety of conditions although not commonly as the dominant species. Dogwood is a very common understory species in the climax forests of the region.

Mature seed of all species was collected in the Durham area during the autumn of 1946 for use the following spring. All seed was stored in a refrigerated room (40° F) until used. The individual treatments were the following: the red and white oak acorns were stratified in periodically moistened sand boxes; the dogwood seed was pulped and placed in moist flasks; the red gum, shortleaf pine, and loblolly pine seeds were stored in dry flasks.

Areas selected for the establishment of plots fell into the following three general categories in decreasing order of light available on the ground: 1. Abandoned fields or similar locations in which *Andropogon* sp. was common in the secondary community typically developed. In some cases it was necessary to select abandoned fields newly planted to pine. 2. Heavily cut-over pine forests which would be classified silviculturally as either a seed tree or a very heavy selection type cut. 3. Pine forests in which the cutting had been very light. These would have been classified as single tree selection type cuttings. In addition, each of these three degrees of light interception was up on two soil textural types, fine-textured soils (loams to clay loams) and coarse-textured soils (loamy sands to

sandy loams). The coarse-textured soils were selected with a deep A horizon so that most of the root system of the seedlings would be growing in the A horizon and so that later mattocking would not mix the A and B horizons. Finally, each of these six soil and light combinations was replicated three times to make a total of eighteen plots.

Each of the plots was selected so that a uniform area 8 x 10 feet was available for work. This small area was the unit plot size. In order to produce differences in soil moisture by reduction in root competition, about one half of the area, 4 feet by 7½ feet, was thoroughly mattocked to a depth of about 8 inches. In the mattocking all roots at the margins of this area were cut and, on the coarse-textured soils, care was taken so that none of the B horizon was brought up and mixed with the A horizon. This preparation was completed in March.

To protect the seeds and seedlings from rodent damage, heavy wire screens of the size of the half plot were constructed. The half plots were further subdivided to provide a reduction in light intensity. The portion to be shaded was determined at random. This quarter plot was the smallest complete unit of the experiment and each quarter plot contained the six species selected for the study. Each species was arranged in a three by three square with 6″ between individuals to prevent serious competition among them. Placement of species within the quarter plot was made at random.

The following planting procedures were used: On mattocked half plots, the seed was inserted in the exposed mineral soil and covered. On the other half plots, the surface organic matter was scraped away and the seeds were inserted in the mineral soil and covered as before. The organic material was then returned to the unmattocked half plot. The planting depths used varied with the species. The pines were planted ¼-½″ deep with 6 to 8 per hole. Red gum was planted the same depth with 15 to 20 seeds per hole. Dogwood seeds were planted ½-¾″ deep with 8 to 10 seeds per hole. The oak acorns were planted 1-1½″ deep with 3 to 4 to a hole. After each half plot was completely planted, the rodent screen was placed over it and fixed in position with stiff wire pins, and the apron of the screen was covered with soil. This planting was completed between the 25th and 31st of March.

Beginning the 25th of April, the plots were checked once a week for germination and the germination time for each seedling was noted. As soon as a fair number of seedlings had come up on each plot, the rodent screens were lifted, and the seedlings were thinned. To avoid bias, only one seedling was allowed to persist in each of the nine planting holes; the one selected being the one farthest from the center of the three by three square. Several weeks after the first germination, an attempt was made to transplant seedlings into holes where none had emerged. Later observations showed these transplants to be inferior to the undisturbed seedlings in every way and they were not considered in the final analysis.

Two weeks after the first seedlings had come up the shading of the quarter plots was begun. This was done by sewing two thicknesses of a thin, loose weave cotton cloth over the rodent screen.

The date of death of the seedlings was always recorded along with the cause where that was determinable.

Soil moisture measurements were taken twice during the growing season. The first sampling was started on June 7, four days after the last previous general rainfall. The second was taken on August 14, five days after the last previous rain. Measurements were taken with the soil auger at three depths: 2-3″, 5-7″, and 10-12″. They were taken at several random locations on the unshaded portion of each of the 36 half plots. The soil moisture collections were oven-dried at 110° C and the moisture per cent expressed on the basis of dry weight. While no quantitative estimates of the amount of water available to the seedlings are possible with these collection methods,

it is felt that they do give adequate relative measures of the amount of soil water available to the plants between rains. It is during this period that soil moisture must become limiting in survival and growth.

Soil samples of the A_1 horizon were taken at each of the plot locations. These samples were air-dried, ground, and passed through a 2 mm sieve. Moisture equivalent (Briggs and McLane 1907) was determined by the use of the centrifuge. To determine permanent wilting percentage oat seedlings (*Avena sativa* L.) were grown in paraffined containers and allowed to reach a height of four to six inches. Then the surface was sealed with paraffin and the plants allowed to wilt. This wilting was carried to a point which would correspond to the ultimate wilting point (Taylor, *et al.* 1934). The moisture percentage at this point was determined.

The soil moisture at the 2-3 inch level was of particular interest since the young seedlings would obtain most of their moisture from this level. The soil moisture percentages for the June 7 collection were converted to relative wetness (Conrad and Veihmeyer 1929) by dividing the field moisture percentages by the corresponding moisture equivalents. This operation places the soil moisture percentages on a comparable basis regardless of soil texture. One method of obtaining a figure for the amount of soil moisture available to the seedlings is to subtract the wilting percentage from the field moisture percentage. This was done for the 2-3 inch level for the June 7 collection, and the resulting figures are referred to as the available soil moisture percentages.

Radioatmometers (Livingston 1911) were used for most of the light measurements in the experiment. Certain valid objections have been raised against the use of radioatmometers for light measurements (Shirley 1931). However, they were to be used only on a relative basis and there seemed to be no serious objection to their use. They were set up as follows: paired black and white atmometer bulbs held on bottles of water were placed so as to get a good representation of the light falling on a plot. Early in the day both black and white bulbs with bottles were weighed to the nearest $\frac{1}{10}$ gm. Sometime near sunset the bottles were weighed again to obtain the evaporational loss. The measurements were continued for two or three days for each plot. Corresponding measurements were taken at a control location in full sunlight at one of the open field plots which were all considered to receive 100 per cent of full sunlight. Measurements were avoided on cloudy or variable days. Evaporation figures for the bulbs were corrected for variation in bulb surface areas, and the difference between the black and white bulbs was taken as the amount of evaporation caused by radiation. These figures for each plot were divided by the appropriate figure for the control plot to give an approximation of the percentage of full sunlight falling on the shaded plots.

To determine the amount of light reduction due to the rodent screens and shading cloths, measurements were made with a Weston illuminometer. The rodent screens reduced the intensity to 66 per cent of full sunlight, and this was the maximum received by any seedling. The shading cloth reduced the light by another 47 per cent and both corrections were applied to obtain true relative light intensities for the plot.

During the months of December and January all of the living seedlings on the plots were removed from the ground, tagged, washed free of soil, dried at 70° C. for 48 hours, and weighed.

Results

A summary of the data describing the physical environment for the experimental plots is given in Table I. Included are such soil, available soil moisture, and light data as were used later in the statistical analyses.

TABLE I. *Summary of physical data for plots*

Stand condition	Light as percentage of full sunlight		Ultimate wilting percentage of A horizon	Available soil moisture percentage at 2-3 inch level on June 7		Moisture equivalent percentage of A horizon	Relative wetness of 2-3″ level on June 7	
	Unshaded portion	Shaded portion		Mattocked plot	Undisturbed plot		Mattocked plot	Undisturbed plot
Coarse-textured soils								
Open field	66	35	1.0	7.8	4.7	10.2	86	56
Open field	66	35	0.7	3.3	3.8	5.1	78	88
Open field	66	35	1.0	6.9	4.4	7.6	104	71
Heavy cut	55	29	2.0	15.5	7.8	12.0	146	82
Heavy cut	56	29	2.4	11.9	10.2	12.7	112	98
Heavy cut	46	24	1.6	16.2	12.4	11.7	152	120
Light cut	4	2	1.1	12.1	7.9	7.6	174	118
Light cut	14	7	1.4	16.5	7.7	9.1	197	100
Light cut	18	9	2.4	12.8	3.5	11.6	131	51
Fine-textured soils								
Open field	66	35	5.1	16.7	9.6	26.3	83	56
Open field	66	35	3.4	14.2	13.2	16.7	105	99
Open field	66	35	4.4	10.0	3.4	18.0	80	43
Heavy cut	43	23	4.4	8.9	6.7	23.0	58	48
Heavy cut	37	20	9.4	12.1	7.3	28.0	77	60
Heavy cut	18	9	9.2	19.3	10.6	26.0	110	76
Light cut	22	11	4.8	7.8	6.3	32.5	39	34
Light cut	21	11	8.6	12.8	7.5	33.5	64	48
Light cut	12	6	10.5	17.5	9.8	27.5	102	74

Rainfall and soil moisture data

Rainfall data for the Duke Forest during the summer of 1947 were supplied the writer by Dr. Harold E. Young. There was an even distribution of rainfall through the summer months; at no time did drought conditions prevail. In Table II, the rainfall data have been summarized by months for comparison with records of average rainfall at Durham. The comparison reveals the summer of 1947 to be slightly wetter than average. Moreover, the distribution was not normal. The early portion of the growing season, from the middle of April to the end of May, was drier than average, whereas the latter part of the summer and early fall were wetter than average. This rainfall pattern would tend to throw more than normal moisture stress on the seedlings early in the growing season and to increase mortality during that period. The converse would be true in the latter part of the growing season.

TABLE II. *Comparison of rainfall data for summer, 1947, with 17 year average for Durham, North Carolina (Hambidge 1941)*

Period	Rainfall, 1947 in inches	Rainfall, 17 year average in inches
Last half April	1.09	1.72
May	2.38	3.16
June	4.57	4.08
July	2.94	4.42
August	3.41	4.85
September	5.33	3.08
First half October	3.96	1.38
Total	23.68	22.69
Total for mid-April to June 1	3.47	4.88
Total for September 1 to mid-October	9.29	4.46

The relative wetness figures were subjected to regression analysis using the latter figures as the dependent variable and moisture equivalent and light as the

independent variables. The data for mattocked and undisturbed plots were analyzed separately. The analyses of variance for these regressions are given in Table III.

TABLE III. *Analysis of variance of regression on relative wetness with moisture equivalent and light percentage as variables*

Source of variation	Undisturbed plots: Degrees of freedom	Sums of squares	Mean square	F ratio
Moisture equivalent	1	4051	4051	8.65‡
Light percentage	1	395	395	
Error	15	7036	469	
Total	17	11482		

Source of variation	Mattocked plots: Degrees of freedom	Sums of squares	Mean square	F ratio
Moisture equivalent	1	11192	11192	16.86†
Light percentage	1	7942	7942	11.96*
Error	15	9966	664	
Total	17	29100		

*significant at the 1% level.
†Significant at the 0.1% level.
‡Significant at the 5% level.

On the mattocked plots, both the moisture equivalent of the soil and the light percentage on the plot were related to relative wetness, while on the undisturbed plots only moisture equivalent was related to relative wetness. The regression equations show that these relations are negative. In other words, the relative wetness of the coarse-textured soils was higher than that of the fine-textured soils and, the mattocked plots, the relative wetness of the soils in the open areas with high light intensities was less than in the shaded areas with low light intensities.

Several factors probably explain the effect of soil texture expressed as moisture equivalent. In the first place, the actual field capacity of coarse-textured soils is higher than the moisture equivalent, and it may be seen from Table I that a number of coarse-textured soils were considerably wetter than the moisture equivalent on June 7, four days after the last previous rainfall. In the second place, the last previous rainfall had been only 0.3 inch. For a completely dry fine-textured soil with a moisture equivalent of about 30 per cent, this amount of rainfall would not wet the soil much beyond ⅓ inch. Of course, the soil was not completely dry but on fine-textured soils such a rainfall would not penetrate completely to the depth of 2-3 inches where sampling was done. It would be more likely to penetrate to this depth on coarse-textured soils, however, and they would have a higher relative wetness as a result.

The decrease in relative wetness with increasing light intensities on mattocked plots probably means that with most root competition removed the main factor in water loss is direct evaporation. The evaporation rate would be lower on the more heavily shaded plots and as a result water loss there would be lower than on the exposed plots.

The amount of soil moisture available to the seedlings is a matter of special interest. A summary of average available soil moisture percentages is given in Table IV. The notable difference was between the mattocked and undisturbed plots. In order to see if available soil moisture was related to the other two main factors in the experiment, light and soil texture, a regression analysis was made with available soil moisture as the dependent variable and light and moisture equivalent as the independent continuous variables. The mattocked and undisturbed plots were analyzed separately. The analysis of variance of these two regressions is not shown but neither soil texture nor light was significantly related to available soil moisture in this experiment. This is an important point since available soil moisture can then be used as an independent variable in estimating the effect of soil moisture on survival and growth.

TABLE IV. *Summary of average available soil moisture percentages at 2-3 inch level on June 7*

Open field 8.2		
Heavy cut 11.6	Coarse texture 9.2	Mattocked plots 12.4
Light cut 10.2	Fine texture 10.8	Undisturbed plots 7.6
	Coarse texture mattocked 11.4	
	Fine texture mattocked 13.2	
	Coarse texture undisturbed 6.9	
	Fine texture undisturbed 8.3	

Germination

This experiment was not set up to determine the relative germination under various environmental conditions, so the exact number of seeds planted in each seed spot was not recorded. Still it was obvious from field observation that certain differences did exist between plots, and a summary of seed germination is given in Table V. The percentages in this table were computed as follows: there were nine seed spots for each species in each quarter plot, there were four quarter plots in each area, and 18 areas, making a total of 648 possible seed spots in which seeds of a given species might germinate. The number of spots in which at least one seed germinated was divided by 648 to obtain the percentage.

Since the germination data were not based on careful control in planting, only large differences can be accepted with reasonable certainty and no statistical analysis was attempted. It seems safe to conclude that shortleaf pine, loblolly pine, and red gum seeds all have a higher germination rate in mattocked than in undisturbed plots. This was true despite the fact that all seeds were inserted in the mineral soil. With loblolly pine there appears to be an interrelation between soil texture and soil treatment. On coarse-textured soils there was no difference in germination between the soil treatments while on fine-textured soils there was a considerable difference in favor of the mattocked plots. There was a slight tendency toward better germination in coarse than in fine-textured soils with all species except dogwood. Whether or not this is a significant trend is conjectural.

Survival

In calculating seedling survival percentages, all deaths attributable to causes other than physical environment (such causes as rodent kill, damping off, insect kill, and the like) were eliminated from the basic data. No record of losses due to biological causes is presented because protective measures were imposed upon the plots and such figures would be misleading. The losses were fairly high, especially for the oaks.

In order to represent the percentage survival of the seedlings in an appropriate form for statistical analysis it was necessary to convert the data to probits, the normal deviate corresponding to the observed proportion of living seedlings. The number five has been added to the normal deviates to make all of the values positive. The result of this transformation is to convert the known S-shaped

TABLE V. *Percentage of seed spots in which seeds germinated*

Species	Mattocked coarse-texture	Undisturbed coarse-texture	Mattocked fine texture	Undisturbed fine texture	All Mattocked	All undisturbed	All coarse-texture	All fine-texture
Shortleaf pine.....	52	36	47	27	49	32	44	37
Loblolly pine.....	53	48	51	29	52	38	50	40
Red gum.....	61	33	58	22	60	28	47	40
Dogwood.....	13	8	18	22	16	15	10	20
Red oak.....	93	87	77	72	85	79	90	74
White oak.....	87	87	81	74	84	81	87	77

percentage distribution into a linear one. The probits were obtained from the tables in Fisher and Yates (1943). Conversion was straightforward except for the values 100 and 0 percent. In converting, if 100 per cent had a weight of one, *i.e.*, based on one seedling, this value was considered to be the middle of the class from 50-100 or 75 per cent; if 100 per cent had a weight of two, the value was considered to be the middle of the class 75-100 per cent, and so forth. Similar reasoning applied to the conversion of the 0 per cent figures. The probits were considered as dependent variables and were weighted according to the number of seedlings upon which the percentages were based. The regression analyses of the data were made according to the methods indicated by Fisher (1941). These analyses are considered below by species.

Loblolly pine.—The independent variables chosen for the analysis were the following:

1. The available soil moisture percentage of the 2-3 inch level at the June 7 collection. The June 7 collection was chosen rather than the August 14 collection because there was less available moisture on the earlier date although the available soil moisture percentages showed essentially the same relative distribution on both dates. The available soil moisture percentages for June 7 should give a relative measure of the amount of water available to the seedlings on the various plots during times of slightly deficient soil moisture.

2. The moisture equivalent of the A horizon of the soil.

3. The percentage of full sunlight falling on the seedlings. This was expressed as a linear and as a curvilinear function.

4. The moisture equivalent minus the ultimate wilting percentage.

5. The interaction between the available soil moisture and the curvilinear expression for light percentage.

6. The interaction between the moisture equivalent and the curvilinear expression of light percentage.

Plotting of the data indicated the further possibility of a curvilinear relation between survival and available soil moisture and this relation was shown to be significant. The final analysis of variance for the loblolly pine data is given in Table VIa. Available soil moisture, moisture equivalent, and light percentage all significantly affected survival. The graphs of the regression equation are shown in Figures 1, 2, and 3. For this and all subsequent survival equations, the conversion from probits to percentages is shown on the graphs. Also in these graphs as in subsequent ones all variables save one are

TABLE VI. *Analyses of variance of percentage survival regressions*

Source of variation	Degrees of freedom	Sums of squares	Mean square	F ratio
a. Loblolly pine				
Available soil moisture	1	513,681	513,681	14.6†
Additional effect of Curvilinear form of Available soil moisture	1	186,858	186,858	5.32‡
Moisture equivalent	1	164,466	164,466	4.68‡
Light	1	283,562	283,562	8.07*
Error	55	1,931,699	35,122	
Total	59	3,080,266		
b. Shortleaf pine				
Available soil moisture	1	504,048	405,048	12.7†
Light	1	132,227	132,227	4.16‡
Error	54	1,716,971	31,796	
Total	56	2,254,246		
c. Red gum				
Available soil moisture	1	734,904	734,904	30.6†
Moisture equivalent	1	139,755	139,755	5.83‡
Error	48	1,151,150	23,982	
Total	50	2,025,809		
d. Dogwood				
Available soil moisture	1	98,341	98,341	6.45‡
Moisture equivalent	1	102,430	102,430	6.71‡
Error	26	396,680	15,257	
Total	28	597,451		
e. Red oak				
Available soil moisture	1	134,807	134,807	7.40*
Error	69	1,256,717	18,213	
Total	70	1,391,524		
f. White oak				
Available soil moisture	1	307,902	307,902	15.2†
Error	68	1,380,761	20,305	
Total	69	1,688,663		

‡Significant at the 5% level, *significant at the 1% level, †significant at the 0.1% level.

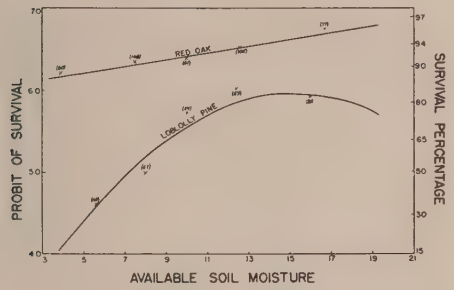

FIG. 1. Survival of loblolly pine and Southern red oak as affected by available soil moisture. Figures in parentheses in this and subsequent graphs represent number of plants upon which point is based.

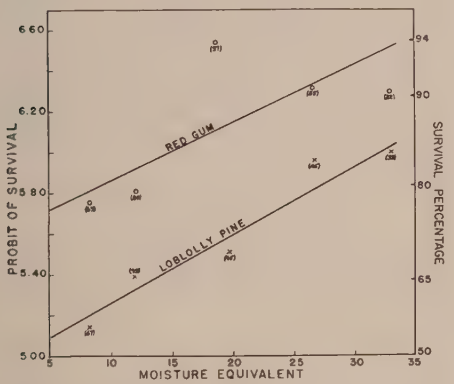

FIG. 2. Survival of loblolly pine and red gum as affected by moisture equivalent.

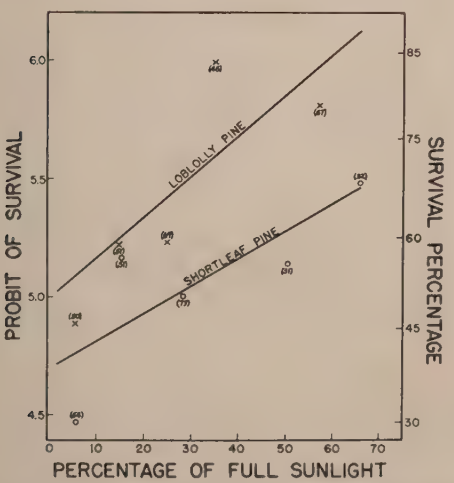

FIG. 3. Survival of loblolly pine and shortleaf pine as affected by sunlight.

set at their mean values while the one under consideration is allowed to vary. The average residual is plotted for successive groups of x.

Shortleaf pine.—The variables used in the regression were available soil moisture, moisture equivalent, light percentage, and the interaction between moisture equivalent and light. The final analysis of variance for the regression is given in Table VIb. Available soil moisture and light were the significant variables. The curvilinear form for available soil moisture could not be demonstrated as with loblolly pine. Graphs of the equations are given in Figures 3 and 4.

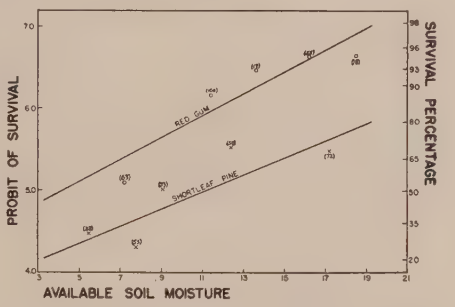

FIG. 4. Survival of red gum and shortleaf pine as affected by available soil moisture.

Red gum.—Here the variables available soil moisture, moisture equivalent, light, and the interaction between light and moisture equivalent were tested. The final analysis of variance is given in Table VIc and graphs of the equation in Figures 2 and 4. Available soil moisture and moisture equivalent were the significant variables. Although the data plotted in Figure 4 would seem to indicate a curvilinear trend, it was not possible to demonstrate this statistically.

Dogwood.—Available soil moisture, moisture equivalent, a curvilinear expression of light, and the interaction between light and soil moisture were tested as variables. As with red gum, the significant variables were available soil moisture and moisture equivalent. The final analysis of variance is shown in Table VId and the graphs of the equations in Figures 5 and 6.

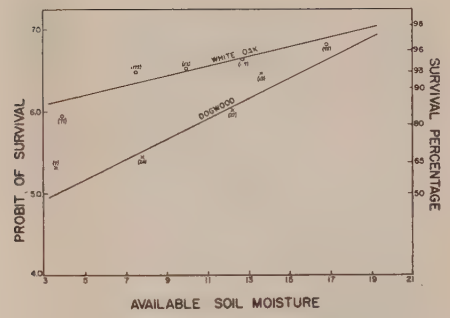

FIG. 5. Survival of white oak and dogwood as affected by available soil moisture.

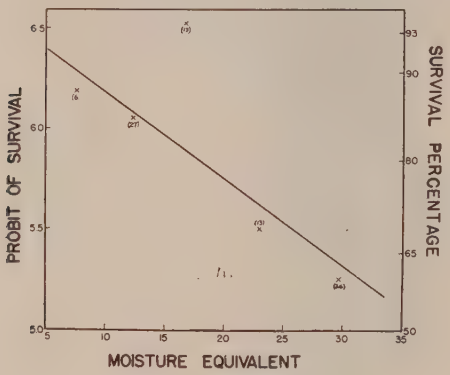

FIG. 6. Survival of dogwood as affected by moisture equivalent.

Red and white oaks.—The variables used were available soil moisture, moisture equivalent, light, and the interaction between moisture equivalent and light. The final analyses of variance are presented in Tables VIe and f and the graphs of the equations in Figures 1 and 5. For both species, available soil moisture was the only significant variable.

Plant weights

To place the plant weights on a comparable basis, the weights were divided by the number of weeks between germination and October 15. The latter date represented an approximate time when growth must have been much reduced due to decreased length of day and temperature. It was also the day on which the oak leaves commenced to change color. The final plant weight figures used on the analyses were the average weight gain per week.

Loblolly pine.—In analyzing the plant weights, they were used as the dependent variables and available soil moisture, moisture equivalent, light, and the two-way interactions between each of the three were used as the independent variables. The plant weights used were averages weighted according to the number of seedlings upon which the average was based. Only light proved to be significant. However, another comparison of the moisture available for growth could be made, and that was the weights on the

TABLE VII. *Analyses of variance of plant weight regressions*

Source of variation	Degrees of freedom	Sums of squares	Mean square	F ratio
a. Loblolly pine, all data				
Light	1	135,659	135,659	8.57*
Mattocked vs. undisturbed plots	1	106,107	106,107	6.70‡
Error	51	807,696	15,837	
Total	53	1,049,462		
Loblolly pine, mattocked plots only				
Light	1	251,249	251,249	13.08†
Error	30	576,197	19,206	
Total	31	827,446		
b. Shortleaf pine				
Light	1	28,549	28,549	13.98†
Available soil moisture	1	12,056	12,056	5.90‡
Light-available soil Moisture interaction	1	10,254	10,254	5.02‡
Error	35	71,484	2,042	
Total	38	122,343		
c. Red gum				
Moisture equivalent	1	411,924	411,924	5.54‡
Available soil moisture	1	352,533	352,533	4.74‡
Error	45	3,347,565	74,390	
Total	47	4,112,132		
d. Red oak				
Logarithm of light	1	14,790	14,790	4.09‡
Moisture equivalent	1	13,242	13,242	3.66
Mattocked vs. undisturbed	1	15,240	15,240	4.22‡
Total due to regression	3	43,272	14,424	3.99‡
Error	67	242,149	3,614	
Total	70	285,421		
e. White oak				
Mattocked vs. undisturbed	1	43,798	43,798	5.49‡
Error	68	542,806	7,982	
Total	69	586,604		

†Signficant at the 5% level, *significant at the 1% level, ‡significant at the 0.1% level.

mattocked versus the undisturbed plots. This comparison proved significant along with light. To determine whether the effect of light was the same on mattocked and unmattocked plots, an appropriate statistical test was made. It was found that an increase in light had no effect on growth on the unmattocked plots while light was related to growth on the mattocked plots. In other words an interaction had taken place; the species was unable to respond to an increase in light intensity at low levels of soil moisture. The final analysis of variance is given in Table VIIa and the equation is graphed in Figure 7. To obtain more easily interpreted figures, the weights shown in this and subsequent graphs of plant weight have been converted to weight at twenty weeks, approximately the length of the growing season.

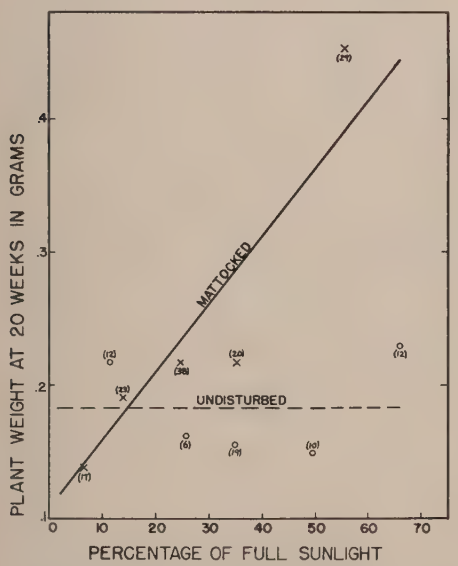

Fig. 7. Loblolly pine plant weight as affected by sunlight on mattocked and undisturbed plots.

Shortleaf pine.—The variables light, available soil moisture, moisture equivalent, the interaction between light and the latter two, and the comparison between mattocked and undisturbed plots were tested for their effect upon plant weight. As is shown in Table VIIb, light, available soil moisture, and the interaction between them were significant. The equations are shown graphically in Figures 8 and 9. In order to illustrate graphically the effect of the interaction between available soil moisture and light, the equation for plant weight without the interaction is shown in dashed lines, and the equation including the interaction is shown in solid lines.

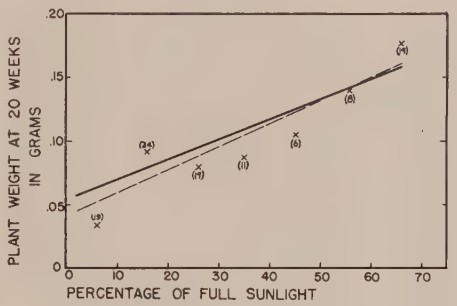

Fig. 8. Shortleaf pine plant weight as affected by sunlight. Solid line shows relation with interaction; dotted line the relation without the interaction.

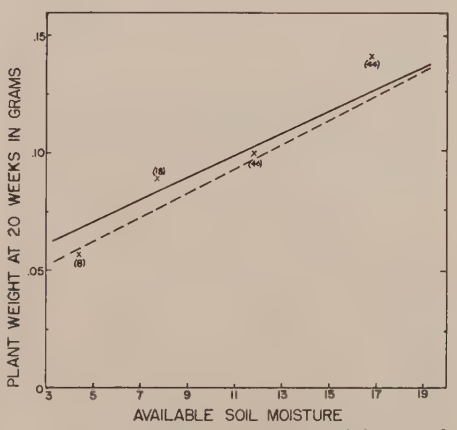

Fig. 9. Shortleaf pine plant weight as affected by available soil moisture. Solid line shows relationship with interaction; dotted line the relation without the interaction.

Red gum.—Available soil moisture, moisture equivalent, light in both linear and curvilinear form, the comparison between mattocked and unmattocked plots, and some interactions between these variables were tested for this species.

Only available soil moisture and moisture equivalent were significant variables.

The possibility that light might give a differential response on mattocked and undisturbed plots was tested and rejected. The final analysis of variance is given in Table VIIc and the equations are represented in Figures 10 and 11.

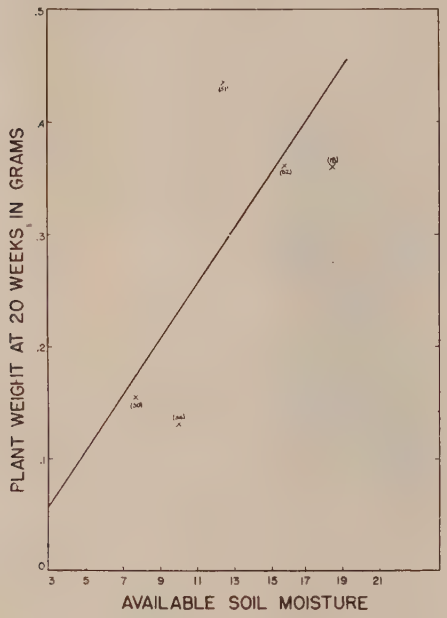

FIG. 10. Red gum plant weight as affected by available soil moisture.

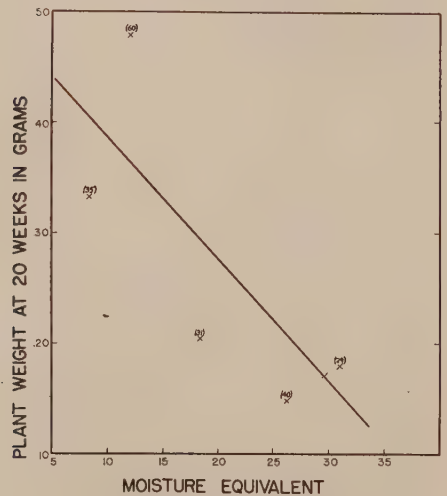

FIG. 11. Red gum plant weight as affected by moisture equivalent.

Dogwood.—It was impossible to demonstrate that any of the variables had any effect upon the weight of dogwood. Either too few plants of the species were available for the establishment of trends, or the species shows little measureable response to environmental conditions over the range encountered in the experiment. Possibly it was a combination of these causes.

Red oak.—In combination, the comparison between mattocked and undisturbed plots, moisture equivalent, and light expressed in a curvilinear form proved to be significant in the case of red oak. It could not be demonstrated that there was a differential response to light on mattocked and undisturbed plots. The analysis of variance is shown in Table VIId, and the equations are graphed in Figures 12 and 13.

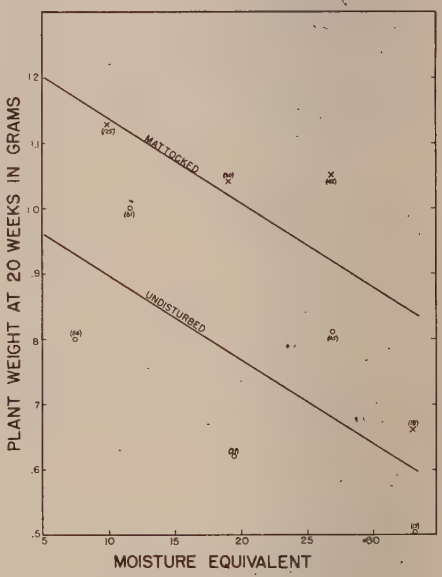

FIG. 12. Red oak plant weight as affected by moisture equivalent on mattocked and undisturbed plots.

White oak.—Only one variable, the contrast between mattocked and undisturbed plots, could be shown to be significant with white oak. There was no demonstrable difference in the effect of light on mattocked and undisturbed plots.

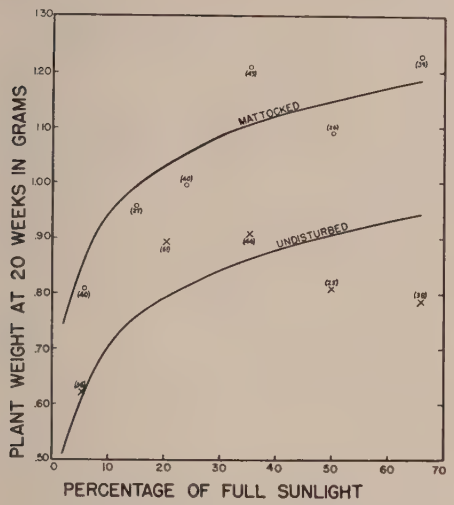

FIG. 13. Red oak plant weight as affected by sunlight on mattocked and undisturbed plots.

The analysis of variance is shown in Table VIIe. Since the variable is not continuous it is not graphed. The plant weight estimate for twenty weeks on the undisturbed plots is 1.74 grams and that on the mattocked plots is 2.13 grams.

DISCUSSION

Survival and plant weight data

Perhaps the best method of comparing the effect of the independent variables on survival and growth within each species and the relative effect between the species is to compare the effect of extremes of conditions from the graphs. The graphs were constructed by setting all variables save one at their mean values for the data for that species. The extremes of the remaining variable were those encountered in the experiment and these extremes are shown in the figures. The calculated differences in survival and plant weights caused by the extremes of one independent variable, as contrasted with the calculated differences brought about by another independent variable should give the relative importance of the two in their effect upon the growth and survival of a given species. To place plant weights on a comparable basis, the differences in weight obtained by comparing extremes were divided by the mean weight of a given species and the differences were then expressed as a percentage of the mean. Survival was already expressed as a percentage, so no conversion was necessary. A summary of the values obtained from the differences in the extremes is given in Table VIII. It should be emphasized that the figures given in Table VIII are idealized values, the best estimates of behavior based on the regression equations.

It is evident that the single most important variable in survival was the relative amount of available soil moisture. For all of the species except the oaks, extremes of the variable resulted in corresponding differences of approximately 50 to 60 per cent in survival, considerably more than any other variable considered. The large seeds of the oaks may be indirectly responsible for the relative insensitivity of these species to the surface soil moisture conditions. The initial impetus given oak seedlings by the large amount of food stored in the acorn must have considerable beneficial influence on their survival capacities. They can immediately extend their root systems and thus draw on soil moisture from considerable depths. On the other hand, the small seeds of the other species dealt with, and the resultant small amount of food available to them from the seed, limit their abilities to extend their root systems upon germination. Consequently they are more sensitive to fluctuations in surface soil moisture. A further explanation for the relatively high sensitivity of a light-seeded species, loblolly pine, to reduced soil moisture is found in the work of Kozlowski and Scholtes (1948). They found that, when growing under similar, favorable conditions, loblolly pine has some inherent limitations in production of both roots and root hairs as compared to certain hardwoods.

It is interesting in connection with soil moisture and its relation to survival to determine the distribution of mortality by months. The distribution figures for the various species, expressed as percentage of total mortality, and adjusted for the

TABLE VIII. *Calculated response of seedlings to extremes of one variable while other variables are at mean values*

Species	Variable at extremes	Range in response	Difference between extremes	Difference as percentage of mean
Survival				
Loblolly pine	Available soil moisture	75—14	61	
Loblolly pine	Moisture equivalent	85—54	31	
Loblolly pine	Light	87—51	36	
Shortleaf pine	Available soil moisture	80—20	60	
Shortleaf pine	Light	68—39	29	
Red gum	Available soil moisture	98—45	53	
Red gum	Moisture equivalent	94—76	18	
Dogwood	Available soil moisture	97—48	49	
Dogwood	Moisture equivalent	92—57	35	
Red oak	Available soil moisture	96—87	9	
White oak	Available soil moisture	98—87	11	
Plant weights				
Loblolly pine	Light on mattocked plots	.444— .119	.325	140
Loblolly pine	Mattocked vs. undisturbed	.267— .161	.106	46
Shortleaf pine	Light	.158— .056	.102	101
Shortleaf pine	Available soil moisture	.138— .063	.075	74
Red gum	Moisture equivalent	.440— .125	.315	106
Red gum	Available soil moisture	.456— .059	.397	134
Red oak	Logarithm of light	.944— .501	.443	47
Red oak	Moisture equivalent	.960— .596	.364	39
Red oak	Mattocked vs. undisturbed	1.056— .816	.240	26
White oak	Mattocked vs. undisturbed	2.130—1.740	.390	20

changing number of seedlings each month are given in Table IX. It is evident that with all species, the period shortly after germination is the one in which maximum mortality occurs. Thus, although June was slightly above average in precipitation, the maximum mortality for all species except red oak occurred during that month. July and August were drier than normal but a comparatively small percentage of the seedlings died during these months. Had June been dry, the losses attributable to soil moisture would probably have been considerably larger.

TABLE IX. *Distribution of adjusted percentage morfality of seedlings by months*

Species	May	June	July	August	September	October
Shortleaf pine	2	62	12	15	7	2
Loblolly pine	2	68	15	13	0	2
Red gum	0	61	15	20	4	0
Dogwood	0	86	0	0	14	0
Red oak	48	31	13	0	6	2
White oak	28	40	13	3	11	5

The two pines were the only species to show sensitivity to variation in radiation intensity in relation to survival. It is probable that this effect is due to the relatively low photosynthetic efficiency of pine (Kramer and Decker 1944) the net result of which is a small root system under the reduced light conditions of the forest. Oosting and Kramer (1946) point out that smaller root systems probably develop under conditions of reduced sunlight, and Kozlowski (1949) presents data which demonstrate this effect. The hardwoods have greater photosynthetic efficiency (Kramer and Decker 1944) and so are relatively insensitive to light variation. In contrasting them with the pines, Kozlowski (1949) reported that the absolute amount of photosynthesis in loblolly pine seedlings was only one-fourth that of overcup oak seedlings. This was true over a large range of light intensities. Mortality due to low light intensities would probably be observed throughout

the growing season in contrast to the effect of soil moisture.

In dealing with the light variable, it is true that the experiment did not cover 100 per cent sunlight and this figure was not used in calculating the responses given in Table VIII. However, examination of the plotted points on a number of the survival graphs will show that the rate of survival increase was beginning to fall off at high levels of light, although this trend was just beginning and was not demonstrable statistically. It appears doubtful if additional light beyond 66 per cent full sunlight would have much further effect upon percentage survival.

Both red gum and loblolly pine responded positively to an increase in moisture equivalent of the soil. In other words, both species survived better on fine- than on coarse-textured soils. This may have been the result of the greater soil moisture available to the plants at many times on finer textured soils, an effect beyond that measured by the available soil moisture data collected in this experiment. Coarse-textured soils would be near the wilting point a greater percentage of the time than would fine-textured soils and red gum and loblolly pine may be particularly sensitive to such variations. The reason for the reverse trend in dogwood is obscure. Perhaps dogwood is more sensitive than the other species to the periods of poor aeration which are more common on fine-textured soils.

The relative effects of available soil moisture or soil treatment and light intensity are quite reversed in their importance when considering plant weights. In all cases where both light and soil moisture contribute significantly to plant weights, the contribution of light is the greater. The difference in favor of light is especially striking with loblolly pine. These findings are in line with those of Shirley (1945) who found that light had more influence upon the plant weights of pine than did soil moisture.

In connection with the effect of soil moisture on plant weight, Wadleigh and Ayers (1945) and later, Wadleigh, Gauch, and Magistad (1946) report a steady decrease in plant weight with decreasing soil moisture. The same trends were evident in the present experiment although a cruder expression of moisture was used. Wadleigh and Ayers (1945) point out that growth reductions at low soil moisture percentages are brought about by reduced hydration of the protoplasmic proteins.

Shortleaf and loblolly pines were the only species to show a demonstrable interaction effect. The inability to show other interactions between the independent variables is of interest in itself. It might be expected that at low available soil moisture levels, the seedlings would be unable to respond in weight to light even though it might be present at fairly high intensities. Schneider and Childers (1941), Loustalot (1945), and Heinicke and Childers (1936) all found that drying of the soil was accompanied by an appreciable reduction in the rate of photosynthesis. The photosynthetic rate fell to about 13 per cent of normal when wilting per cent of the soil was reached in one experiment and the plants did not return to full photosynthesis until two to seven days after having been watered. In dealing with plant weights in the present experiment, such effects should have been evidenced as interactions. In their absence, one explanation suggested is that the seedlings unable to respond died and were thus not included in the plant weights. It may also be that the species failing to show this response were more efficient than the pines in carrying on photosynthesis at low soil moisture levels.

Red gum was the most sensitive species in showing weight response to available soil moisture. Hence one would not expect red gum to grow well, initially at least, on dry sites. Conversely, this checks well with the very fine development of red gum commonly observed in the moist bottomlands of the Piedmont. It is apparent from Figures 2 and 11 that red gum is sensitive to variation in soil texture, showing better development on coarser-textured soils, an effect opposite

from that on survival. There is the anomalous situation of having better survival but smaller seedlings of this species on fine-textured soils. This may be due to the greater amount of energy required for root growth in dense, fine-textured soils. It is difficult to say why this should apply to red gum as well as red oak and not to the other species investigated.

Perhaps a seeming contradiction in the results should be briefly considered. When survival is examined, available soil moisture is the most important variable concerned; when growth figures are considered however, light is the most important variable. Why should these factors differ in their effect in this way? The explanation probably lies in the time during which losses took place. As was shown in Table IX, most of these were early in the season in June before the plant root system was well established. One would expect that soil moisture differences might be most important at that time and the effect of this difference is shown in the analysis. Plant weight figures are based on seedlings which survived the summer and so represent the integrated effect of the environment over this whole period. Apparently light, where the species such as the pines are sensitive to this variable, is more important than available soil moisture in its effect upon plant weight over the course of the season. It follows then that the effect of the environmental factors on survival and plant weight might shift with time. It seems probable that light would become increasingly important. The most important variable in affecting plant weight would in turn have most effect on survival in the following years. This is not, however, to minimize the effect of soil moisture. The data make it clear that it is also an important factor in the determination of plant weight.

Both red and white oak showed some response to soil treatment although, as was true with survival of these species, the effect of that variable was much less than with the other species. It seems likely that the oaks as well as dogwood are more efficient at producing the materials necessary for growth than are the other species. They can carry on their metabolic processes at much lower levels of light and soil moisture than the other species with which the experiment dealt. The well-known ability of the oaks and dogwood to develop in the understory of forests, where soil moisture and light competition are severe, certainly suggests such an explanation.

The most valuable contribution of the plant weight figures from the practical viewpoint is the ability to predict from them the probable success of the seedlings in future years. It seems reasonably certain that large seedlings stand a better chance of surviving than small ones. As Coile (1940) points out, they have larger root systems and can stand unfavorable seasons better than smaller, weaker seedlings. Thus, one would expect a young seedling grown under full sunlight conditions to have a much better chance of subquent survival than those grown under reduced light conditions. To a lesser degree the same statement applies in contrasting the seedlings grown under high and low available soil moisture conditions. It is the cumulative effect of low levels of the two factors, light and soil moisture, which causes the gradual dying out of the moisture- and light-sensitive species, the pines, from the understory of the mature forests in the Piedmont.

It is interesting to consider the results of this experiment in relation to the ecological position of the various species in the successional pattern in the Piedmont. Neither shortleaf nor loblolly pine are important members of the climax community, and of the species investigated they were generally the most sensitive to variations in the environment. Red gum also reacted strongly to variations in available soil moisture and soil texture and it seems significant that this species is not a prominent member of the climax in the area. The three species investigated which are members of the climax, the two oaks and dogwoods, showed rela-

tively little or no response to variations in physical factors. These species which occur in the climax, it seems clear, are more efficient and less demanding in their requirements for survival and growth.

In summarizing the behavior of all of the species, several features need emphasis. One of these is the great diversity of response of the various species to the same environment. Some showed no demonstrable response to a given factor while others were quite sensitive. Even species presumably as similar as loblolly and shortleaf pine were decidedly different in their response to the same variables. No safe predictions can be made about the behavior of one species from that of another. Another feature is the quality of continuous variability in response over the full range of conditions encountered in the experiment. With two exceptions, there was no tendency toward failure in response to one variable merely because of a high or low value for another variable. So far as was determinable, under the conditions of this experiment the effects of the variables were purely additive.

The results of the present study should be accepted with some caution. The trends shown here apply only to first year seedlings and extrapolations for older seedling behavior would not necessarily be valid. It is also true that the analyses of variance indicate that a great deal of variation remains to be explained either by other factors or by a more precise method of expressing the variables treated here.

Silvicultural Applications

From a consideration of the survival and germination figures, it is apparent that the most important initial step one can take to obtain successful establishment of one year seedlings of all the species investigated is to improve the soil moisture conditions. Coile (1940) has pointed out that this may very well be accomplished with the use of a heavy harrow or disk plow to break up the surface organic matter and cut out some of the competing roots in the A horizon. This would seem to be a valuable method for use when a good seed year is in prospect, but it is not desired to make an immediate cut. Shortleaf pine is notorious for its niggardly and infrequent production of seed and this method might be particularly applicable to that species. The use of the fire plow to provide a seed bed in the uncut stand prior to the seedfall should greatly increase the percentage germination on the plowed area, and it is certain that the germinated seedlings would show a very satisfactory survival rate on the plowed ground. The result should be a satisfactory stand of reproduction even under a fairly dense forest. However, the pine seedlings developed under such reduced light conditions will not be of optimum size. It is imperative that the light conditions be improved fairly soon after the seedlings become established or they will be so reduced in size and vigor that their response to release may be slow and inadequate for future survival. Also soil moisture levels will steadily become lower as the early effect of the shallow plowing is nullified by the reinvasion of the roots. Hence an early cut, possibly within two years after the disking, is indicated. This recommendation may be modified by certain conditions of the site and the species. Loblolly pine for example shows sufficient survival response to soil texture so that one might be justified in postponing the cut longer on a heavy textured soil than on a light textured one.

The regression equations in the present paper cannot be used directly in computing the number of seedlings of a given species to be found under certain site conditions even though the environmental factors be accurately measured. It would be necessary to correct them in some way for rodent damage, insect attack, damping-off mortality, and so forth. It is not intended that the data of this experiment be used in such a direct way. Their primary utility should be realized through pointing out trends to be expected under field conditions and thus to help the for-

ester to adapt silvicultural treatment to the needs of the species with which he is dealing.

Summary and Conclusions

In a study designed to determine the independent effects of the variables light, available soil moisture, and soil texture upon the survival and growth in weight of six species of forest tree seedlings, the following information was obtained:

1. Germination data indicated that shortleaf pine, loblolly pine, and red gum all germinated in greater numbers on mattocked areas than on undisturbed areas.

2. The greatest percentage of mortality for all species occurred in early summer, shortly after germination.

3. The data were analyzed by regressions using survival and plant weight figures as the dependent variables, and the measured physical features of the corresponding site as the independent variables. The significant relations are indicated in the following table:

4. Idealized values for survival and plant weight at the extremes of the independent variables were derived from regression equations for each species. Comparisons of these figures within and between species revealed the following: A. The most important variable in determining survival was the amount of available soil moisture. B. The pines were the only species to show survival response to light. This is probably because of the low photosynthetic efficiency of the pines. C. Light was the most important variable in determining growth in terms of weight. D. Red gum was very sensitive to variations in soil texture and available soil moisture. The larger size of this species on coarse-textured soil is in contrast to the better survival on fine-textured soil. E. There is a relatively slight response of the oaks and dogwood to environmental factors. This is probably due to their greater efficiency in producing carbohydrates.

5. The pines are especially sensitive to low levels of both light and available soil moisture, and it is the effect of low levels of these two factors that results in the gradual decline of these two species in the understory of the forest in the Piedmont.

6. The species which show the greatest sensitivity to environmental variations are not prominent in the climax forest, while species showing little or no reaction to environmental variations do occur as members of the climax.

7. The species investigated showed great variation in response to the same variables and consequently no predictions can be made about the behavior of one species from that of another.

Dependent Variables	Species	Independent Variables				
		Available Soil Moisture	Soil Texture	Light	Soil Treatment	Available Soil Moisture-light Interaction
Survival percentages	Loblolly pine	+	+	+		
	Shortleaf pine	+	..	+		
	Red gum	+	+			
	Dogwood	+	−			
	Red oak	+				
	White oak	+				
Plant weight	Loblolly pine	+	..	+	..	+
	Shortleaf pine	+	..	+	..	+
	Red gum	+	−			
	Dogwood					
	Red oak	..	−	+	+	
	White oak	..	..	..	+	

. + = positive relation. − = negative relation.

8. It is pointed out that with two exceptions the effect of the variables was additive regardless of the value for any one of them.

9. Considerable variability in both plant weight and survival figures remains to be accounted for, possibly by other factors and/or by better expressions of the present variables.

10. The present experiment investigated the behavior of one-year-old seedlings and caution should be used in extrapolating these trends.

11. The silvicultural applications of these data are discussed and it is concluded that improving the soil moisture conditions in the forest is the most important initial step in securing satisfactory reproduction of all species. In dealing with the pines, the light conditions must be improved fairly soon after establishment to obtain a young stand of good size.

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BIOLOGY OF FOULING IN THE GULF OF MANAAR: A PRELIMINARY ACCOUNT[1]

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Introduction

A successful anti-fouling research program has its basis on a detailed knowledge about the biology of the attaching organisms, their occurrence, seasons of settling, frequency and mode of attachment and rate of growth in the particular habitat. Although many inquiries have been initiated in the more advanced countries, the subject in general has been neglected in tropical and sub-tropical areas, in spite of the great practical utility of such studies in navigation and other allied topics. It would seem necessary that more attention should be directed in this field than hitherto paid. The present communication is one among a series of papers by the author dealing with the important organisms collected from the monthly collectors exposed at Krusadai Island (Pamban Port). The attachments on panels recorded through a period of one year have been reviewed.

Materials and Method

In the preliminary investigations conducted elsewhere to study the rate and seasons of attachment of the different organisms, non-toxic panels were hung in the sea from a raft to receive the settlement. The methods employed during this investigation were similar. The non-toxic collectors used were different kinds of wood blocks, each with a surface area of 288 sq. in. The blocks were hung from the Krusadai Oyster "raft" being submerged about a fathom from the water line.

Although the necessary period of exposure of panels has been found to vary from two to forty-four weeks in the other localities where similar observations have been made, an average of one month's submergence is the general recommendation for the tropical environment. This interval of exposure was adopted first. The time of submergence initially adopted was found to yield satisfactory results in so far as the amount of distinguishable organisms attached on the panels was concerned and hence was continued through the present study.

After exposure the growth on the blocks was examined with the aid of a lens and the organisms were listed. The growth was then scraped off and the total volume of attachment on each block was determined by the displacement method. The blocks after drying were reintroduced for the collection of organisms.

The succession in the appearance of organisms was observed on a separate set of panels which were examined every ten days.

Physical Features of the Habitat

Krusadai Island[3] (Lat. 9° N and Long. 79° E) is one among the string of islands in the Gulf of Manaar. The climate is tropical. Lying as it does at the "head" of the Gulf, where it opens into Palk Bay through the Pamban pass, the effects of changes in hydrographic conditions of both seas are reflected in the waters around Krusadai Island. The two prevailing monsoons are the South-west during June to September and the North-east from October to December. The latter alone is rain-bearing. The monthly averages of daily observations of air temperature, surface temperature and spe-

[1] Contribution from the Marine Biological Station, Krusadai Island, Pamban, Gulf of Manaar. Published with the kind permission of the Director of Fisheries, Madras.

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[3] A detailed account of the physiography of Krusadai Island is available in the "Littoral Fauna of Krusadai Island." *Bull. Mad. Govt. Mus., Nat. Hist. Ser., Vol. I, No. 1,* 1927.

cific gravity are recorded in Figures 1 and 2. The total rainfall for each month is illustrated in Figure 3.

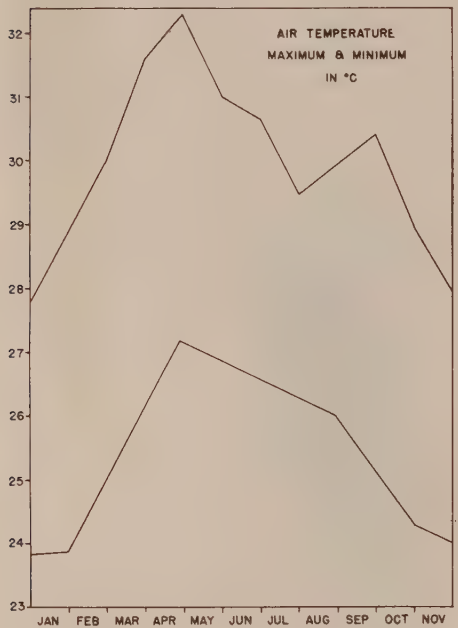

FIG. 1. Monthly averages of daily observations of maximum and minimum air temperature.

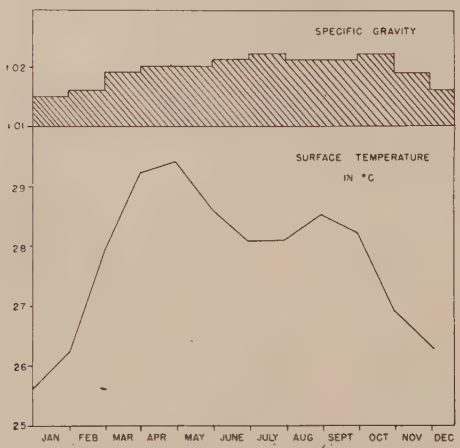

FIG. 2. Monthly averages of daily observations of specific gravity and surface temperature of Krusadai Sea.

ATTACHMENT OF ORGANISMS

The attachment of organisms on surfaces, particularly in the colder areas, has been found to form three distinguishable stages (Harris 1943). They are: (1) bacterial slime, (2) diatom flora, and (3) attachment of higher animals. Thus a bacterial slime constitutes the initial settlement on the exposed areas, with diatoms, algae, hydroids and other higher animals following in that order of appearance. That bacteria form the initial film on surfaces has been corroborated by American workers as well (Phelps 1942; Scheer 1945; Weiss 1948). Investigations in Australia have however revealed that diatoms replace bacteria in forming the first settlement (Wood 1950).

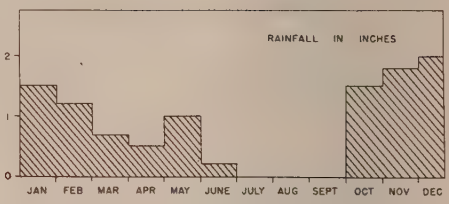

FIG. 3. Total rainfall for each month.

Mention has already been made of the examination of ten-day blocks. This set of panels was introduced to learn the probable stages in the settlement of organisms. However, it has not been possible to distinguish the existence of separate stages in settling. Although a certain amount of primary film is formed, consisting probably of both bacteria and diatoms, the other organisms either settle simultaneously or follow immediately.

ORGANISMS REPRESENTED

Below are given the organisms that were noticed to attach on these monthly collectors. The list is in no way complete or exhaustive. Probably many of the minute individuals have been omitted. The seasons of attachment of the important organisms have been given. It is beyond the scope of the present communication to deal in detail with the biology of the different attaching forms.

Protozoa

Very few protozoans were noticed among the attached organisms. The chief among those present are the stalked cili-

ates, *Epistylis* and *Zoothamnium*. They were present all year around.

It has to be suggested that the technique followed during the present study may not be suitable to assess the importance of protozoans as attaching organisms. The magnification possible with a lens would hardly be sufficient to distinguish and identify many of the smaller forms, which, as a result, may have been left unnoticed.

Sponges

Very few sponge encrustments were noticed on the collecting panels and even those present could not be positively identified due to their small size. The time of submergence of the collectors may not have been sufficient for the sponges to attain a distinguishable size.

Hydroids

Although a large number of hydroids have been recorded from this locality[4] the common species that attached to the collectors were *Pennaria disticha* Goldfuss and *Lytocarpus philippinus* Kirchenpauer, the thecate form predominating. *Lytocarpus* was outstanding during the seasons of monsoon, while *Pennaria* presented inconsistencies in its occurrence. The first period of dominance of the latter species was in March and the second in June.

Polyzoans

Polyzoan colonies formed a large proportion of the growth on the blocks especially during the monsoon seasons. *Thalamporella rozieri* Audouin was common in the months of July and August and the calcareous *Membranipora* sp. in August.

Mollusca

The rock oyster, *Ostrea cucullata* Born, was the main attaching mollusc, appearing on the collectors almost throughout the year. The bivalves *Pinna* sp. and *Pteria* sp. were also noticed to attach on the blocks. The frequency of occurrence of the latter species was greater during the months from June to September (South-west monsoon season).

The molluscan borers *Martesia* sp. and *Teredo* sp. were noticed to bore into some of the blocks exposed for collection. Their appearance on the collectors was not restricted to any particular season and hence there is every reason to believe that the waters contain the active larvae of these two species throughout the year. It was, however, observed that the growth of *Teredo* was retarded during the months of rainfall probably due to lowering of the salinity of the Gulf waters.

Annelida

Although various species of Chaetopods appear on the blocks, *Dasychone cingulata* Grube was perhaps the only sedentary polychaete which attached to the experimental blocks. This tube builder appeared on the panels in the months from February to May.

Crustacea

Cirripedia. The acorn barnacles were perhaps the most numerous and conspicuous organisms on the collecting panels. The species of *Balanus* that were responsible for the fouling were *B. amphitrite* and *B. tintinnabulum.*

Two varieties of *B. amphitrite* identified among the fouling organisms were *B. a.* var. *venustus* Darwin and *B. a.* var. *denticulata* Broch. Var. *venustus* was most common in all the seasons although peaks in its frequency of occurrence coincident with the monsoons could be recognized. Var. *denticulata* was less abundant and the appearance was restricted to the months January and July to September. *B. tintinnabulum* attached to the panels from June to September.

The stalked barnacle *Lepas anserifera* was present in the months of July and August.

Other Crustacea. In addition to the barnacles there were a number of other crustaceans attaching on the blocks. Copepods, amphipods, isopods and cyprids were met with throughout the year. The

[4] "Littoral fauna of Krusadai Island," *op. cit.*, pp. 7-20.

mud-tube-building amphipod *Corophium* was the chief among the crustacean visitors on the blocks.

Tunicates

The compound ascidian *Diandrocarpa brackenhielmi* Michaelsen and the small dull reddish leathery ascidian of the genus *Polycarpa* Heller were the fouling tunicates recorded from the blocks in the months of July and August, the former being comparatively abundant.

Diatoms

Although many sedentary diatom chains were noticed on the panels, none of them could be positively identified due to the meagre knowledge of the systematics of sedentary forms. Listing these had to be reserved for a subsequent study. The importance of the appearance of diatoms on the panels exposed has been well realized in so far as they probably serve as food for many of the higher attaching organisms.

Algae

Algae were rather poorly represented on the collecting panels.

Growth in Different Months

That the fouling would be more severe in certain seasons than others is only a reasonable assumption. The rate of settlement can be assessed by determining the amount of attachment on a uniform area of exposed surface maintained throughout the different seasons. In this instance the volumetric method was followed and results are shown in Figure 4. The attachment in the months from July onwards was particularly abundant.

Discussion

From this preliminary study it is not possible to arrive at any definite conclusion. However, several significant details have come to light during the course of this investigation. Although the amount of settlement would depend on the surface preference of the individual organisms for attachment and growth and the competition for space, a general picture of the probable seasons of settling of the major fouling organisms has been made available by this study. The months of monsoons appear to be favorable seasons for attachment. In addition to the possibility of these seasons being coincident with the breeding intensity of the different organisms, the currents in the Gulf also probably aid the wide distribution of the larvae of the attaching forms.

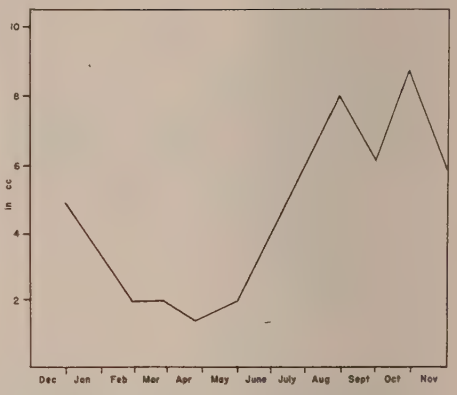

Fig. 4. Volume of attached organisms.

Summary

The major fouling organisms in Krusadai Sea have been listed. Their seasons of incidence have been detailed and the amount of attachments in the different months compared. Fouling is most intense during the monsoon seasons from July to September and from October to December.

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THE RATE OF APPARENT PHOTOSYNTHESIS OF SOME BROADLEAF EVERGREENS

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The ability of a plant to maintain itself in a given environment is effected by all of the factors which affect its rate of vegetative growth and reproductive development. Since the factors of a particular environment, such as light or temperature intensity, duration, or sequence may effect the growth and developmental responses of a plant differently, it is obvious that a combination of factors which lead to good growth will not necessarily result in reproductive development. However, if the factors which initiate development are present, then a knowledge of the factors affecting growth would be of value in predicting the success of the plant in the environment.

The vegetative growth of a plant, although conditioned as to its rate by factors such as temperature and moisture, is ultimately related to its ability to manufacture more food than it uses. In a general way then, if the rate of respiration is not excessive and other factors not limiting, the growth of a plant can be directly related to its rate of photosynthesis and to the factors affecting that rate. That this is so is attested by the results of many experiments in which the rate of growth was proportional to the factors affecting the rate of photosynthesis as, for example, light intensity (Arthur and Porter 1935, Blackman and Matthaei (1905, Burns 1923, Shirley 1929) ; carbon dioxide concentration (Cummings and Jones 1920, Reid 1930, Wilson, Fred, and Salmon 1933, Georgi, Orcutt, and Wilson 1933, Johnston 1935, Bolas and Melville 1935) ; temperature (Matthaei 1905, Lundegårdh 1924, Stalfelt 1937, Werner 1934). Most of these experiments, however, were performed on plants growing under laboratory conditions or were generally of such short duration that the data cannot be used to estimate the performance of the plants under natural conditions. Apart from the work of Heinicke (1937) on a single apple tree, and the studies of Thomas and Hill (1937) on groups of alfalfa and wheat plants, the writer is unaware of any studies in which the rate of photosynthesis was determined over an extended period of time on plants growing under natural conditions. It was felt that if such a study were undertaken on at least two species of plants growing under the same environment, the photosynthetic responses of the plants when correlated with the coincident light, temperature and humidity might afford an understanding of their growth responses under various climatological regimes.

METHODS

Since the experiment was planned to extend through one winter, two broadleaf evergreens which normally have a somewhat different geographical distribution were chosen. *Camellia japonica* L. (camellia) and *Ligustrum japonicum* Thunb. (privet) were the species used. Three plants, approximately three years old, of each species were placed in fourteen inch pots. The potted plants were then placed on a platform, located near the writer's laboratory, so that none of the plants shaded each other.

The rate of apparent photosynthesis was determined by measuring the amount of carbon dioxide present in the air before and after it had passed over the leaves of the experimental plants. The difference between the two readings was taken as a measure of the carbon dioxide used by the plants. The carbon dioxide content of the air was determined by passing the air stream through absorption towers and measuring the change in conductivity of the absorbing solutions. Waugh (1937).

Celluloid envelopes, into which the

leaves to be tested could be placed, were connected by copper tubing to the absorption towers. The envelopes were tested for eddy effects with smoke and since no dead space was apparent, it might be assumed that the air stream would pass over the entire leaf surface. During photosynthetic measurements the air within each envelope was renewed in approximately .8 seconds at a rate of 2.5 liters per cm^2 of leaf surface per hour. The celluloid was sufficiently thin so that no appreciable reduction of the light intensity was apparent. The temperature of the leaves within the envelopes was compared with leaves outside of the envelopes by means of a thermocouple. When air was moving through the envelopes, as in photosynthetic measurements, the temperature of the leaves within the envelopes was approximately 1° C higher than the normal leaves. These determinations were made on a day of high light intensity. When the light intensity was low, there was no measurable difference in temperature between the leaves. When photosynthetic measurements were not being made, an air stream was passed back through the lines, so that the leaves within the envelopes would not be subjected to excessive temperatures.

Five leaves from three plants of privet and four leaves from three plants of camellia were used. These leaves were chosen so that the total area for each species was approximately 50 square centimeters. Although the same leaves were used for a period of more than six months, they did not exhibit any damage or abnormality at the end of the experimental period.

Photosynthetic determinations were made on both species of plants on approximately 40 days of the experimental period, which extended from November of one year to May of the following year. Determinations were of ten minute duration, each half hour of the day, from approximately one hour before sunrise to one hour after sunset.

It should be noted that the measurement of the apparent rate of photosynthesis was particularly useful for the purposes of this experiment. Such determinations underestimate the rate of photosynthesis by the amount of carbon dioxide produced in respiration and as such provide a much truer picture of the net assimilate available for growth. Respiration measurements, made while the plant was not exposed to light, indicated that the rate for the two species was of the same magnitude. Thus, the measurements obtained during the daylight hours should afford a good measure of the net accumulation of both species under similar conditions.

Light was measured by a radiometer devised by the writer (Wilson 1948). Two radiometers were placed on the platform near the plants and were connected in series to a recording potentiometer. The temperature and the relative humidity records were obtained by use of a Friez hygrothermograph located in a standard weather bureau type instrument shelter which was adjacent to the platform on which the plants were kept.

Results

More than three hundred measurements of the rate of apparent photosynthesis of both species of plants together with concurrent measurements of the light, temperature, and relative humidity were made from November to May. Since the publication of so many raw data hardly seems justified in this short paper, regression equations were prepared from the data in which the rate of apparent photosynthesis as mgm $CO_2/100cm^2/$ hr. was the dependent variable and the following factors or combinations of factors tested for their contribution as independent variables. The factors tested were temperature, light, light times temperature, vapor pressure deficit, and light times temperature times vapor pressure deficit. As might be expected, temperature alone was not significant, nor was vapor pressure deficit. Obviously these factors could only act upon the rate of photosynthesis when light was present,

so that light and the combinations indicated above proved to be significant as the independent variables. When the various variables were tested by an analysis of variance they proved to be very highly significant, *i.e.,* beyond the .1 per cent level.

The equation for camellia is:

$$Y = -.005X_1 + .0025X_2 - .0001X_3$$

The equation for privet is:

$$Y = .025X_1 + .0014X_2 - .00006X_3$$

where X_1 is light as per cent of full sunlight, X_2 is the per cent of light multiplied by the temperature in degrees centigrade plus five since $-5°$ C was the lowest temperature during the experiment, and X_3 is the light multiplied by the temperature multiplied by the vapor pressure deficit. The standard error is, as one would expect, quite large, approximately, 15 per cent. However when one considers all of the possibility for error in an experiment of this type, it is far from unreasonable.

An examination of the equations indicates that although all of the photosynthetic determinations were performed at the same time under similar conditions the response of both species was quite dissimilar. With respect to the direct effect of light, camellia had a negative and privet had a very strongly positive coefficient. While at first glance this would seem to indicate that camellia carries out photosynthesis in the dark, it merely signifies that in this species temperature has an important modifying effect. There seems little question, however, that camellia is unable to stand as high a light intensity as privet and still maintain a high rate of photosynthesis.

The response of both species to the light-temperature interaction is, of course, positive. The larger value for the camellia coefficient indicates that a higher temperature is more important for a higher rate of photosynthesis than in privet. It does not seem to the writer that this necessarily indicates that privet is a low temperature plant but rather that a high temperature is not as important in maintaining a high rate of photosynthesis.

Finally, the three way interaction is negative for both species. As one would expect, as the vapor pressure deficit increases the rate of photosynthesis decreases. It is, of course, no novelty to point out that as the leaf tissues are exposed to conditions which favor desiccation the rate of photosynthesis tends to decrease. Here also, as in respect to the other two variables, there is a pronounced species response. Camellia is almost twice as adversely affected by an increasing moisture deficit.

In order to show more clearly the differential response of the two species, Table I was prepared, by means of the equations, showing the calculated photosynthetic response under divergent environments. The values chosen for light, temperature, and vapor pressure deficit might represent a fair cluster of conditions for a winter and a summer situation.

TABLE I. *The rate of apparent photosynthesis in mgm CO_2/100cm²/hr., of camellia and privet under varying summer and winter conditions*

Rate of photosynthesis		temperature	light	v.p.d.
camellia	privet			
1.4	1.1	25° C.	20%	5mm.Hg.
.5	.8	25° C.	20%	15mm.Hg.
3.9	4.0	25° C.	70%	5mm.Hg.
1.7	2.8	25° C.	70%	15mm.Hg.
.3	.7	5° C.	20%	5mm.Hg.
.1	.5	5° C.	20%	10mm.Hg.
1.0	2.5	5° C.	70%	5mm.Hg.
.3	2.0	5° C.	70%	10mm.Hg.

DISCUSSION

The results described above clearly indicate that the rate of apparent photosynthesis for both species respond differently to similar conditions. The figures of Table I suggest that camellia not only has a higher temperature requirement but that it is much more adversely affected by a high vapor pressure deficit. The data do not indicate that light by itself is harmful to camellia since at high temperature and light and low v.p.d. both species pho-

tosynthesize at practically the same rate. Under the same temperature and light but high v.p.d. however, the rate of photosynthesis of privet is almost twice that of camellia. It would seem that the major factor operating to produce the difference in response is the effect of moisture upon the photosynthetic mechanism.

The conditions under which both species are commonly planted indicates that there are real differences in their moisture requirements. Camellias are mostly planted, in Georgia, where they will receive partial shade for at least half of the day. It is usually recommended that they be heavily mulched and that during a dry spell they be given frequent watering. Privet is commonly planted where it will receive full sun for the entire day and the writer has never observed a privet plant suffering from lack of the special treatment during a drought that camellia requires. These observations are confirmed by Bailey (1947) who records that, "camellias . . . flower best in half-shady somewhat moist places. A mulch . . . and thorough watering during the dry season several times a week start the bushes into a vigorous and healthy growth." Concerning *L. japonicum* he noted that, ". . . it may be grown as far north as Philadelphia," and that, "the privets grow in almost any type of soil and even in rather dry situations."

The cause for the different moisture requirements has not been determined. The writer has had occasion to transplant a number of plants of both species and has noted that the root system of privet is much more extensive than that of camellia.

It would appear that the equations describing the rate of apparent photosynthesis as affected by certain environmental factors also describe the general growth responses of both species. Between the extremes of environmental conditions which would cause specific protoplasmic damage the rate of growth closely parallels the rate of apparent photosynthesis. Similar equations if derived for other species of plants might have value in determining both the minimum and optimum growth under varying environmental conditions.

Summary

1. More than 300, ten minute, measurements of the rate of apparent photosynthesis of *Ligustrum japonicum* and *Camellia japonica* growing under natural conditions from November to May were obtained, together with data on the light, temperature and vapor pressure deficit.

2. Regression equations were calculated describing the effect of the environmental factors on the photosynthetic rate of both species and a difference in response between the species was noted.

3. Interpretations of conditions affecting growth from the equations agreed well with other information concerning the factors affecting growth and distribution of both species.

4. It is suggested that similar studies on other species might be of value in relating the factors affecting photosynthesis to the normal distribution of the species.

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EXPERIMENTAL BACKGROUND TO THE STUDY OF THE DISTRIBUTION AND ABUNDANCE OF INSECTS

I. THE INFLUENCE OF TEMPERATURE, MOISTURE AND FOOD ON THE INNATE CAPACITY FOR INCREASE OF THREE GRAIN BEETLES.[1]

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Introduction

It is well known that in nature many species of insects vary in numbers from place to place at any one time, and in any one place their numbers fluctuate with the seasons. They tend to increase in numbers in favourable places or if we consider their numbers in one place they tend to increase during favourable seasons and to decrease during unfavourable seasons. Distribution from place to place and abundance at different times are two aspects of the one fundamental problem.

Other things being equal species which can increase in numbers rapidly during the favourable periods will be more abundant than those which increase in numbers slowly. Thompson (1939) was aware of this and he pointed out that "the complex of factors which actually affect control in the case of any one species differs in composition from point to point and year to year in the area of distribution." Davidson and Andrewartha (1948) were able to identify the major factors determining numbers of *Thrips imaginis* in South Australia as they fluctuated from season to season. In any one year the number reached was a race against time, depending chiefly upon the extent of the favourable season. On the average the physical environment remained favourable for too short a period for the insects to increase to a point where competition became important. The complex of factors causing fluctuations in this and other natural populations can only be discovered by the ecologist who is prepared to study the natural population of insects in the field. Nevertheless, certain concepts derived from laboratory experiments can form a useful background for such field studies.

One such concept is the innate capacity a species has to increase in numbers. A species which has a high capacity for increasing in numbers may reach larger numbers in favourable situations (or in favourable seasons) than the species with a low capacity for increase. In a previous paper (Birch 1948) reasons were given for choosing, as the most appropriate measure of an insect's innate capacity for increase, the index which Lotka (1925) called "the intrinsic rate of natural increase."

The intrinsic rate of natural increase (r) is the infinitesimal rate of increase which a population of *stable age distribution* would have when growing in a constant environment in which space was unlimited:

$$\frac{dN}{dt} = rN.$$

or in the integrated form:

$$N_t = N_o e^{rt}$$

where N_o is the number of animals at time zero and N_t is the number of animals at time t.

The *stable age distribution* is a particular sort of age distribution; its characteristics have been discussed elsewhere (e.g. Lotka 1925, Birch 1948), and need not be discussed at this point.

Notwithstanding the fact that natural populations never possess a stable age distribution nor a stable environment the innate capacity for increase (r) is a very useful concept for background experimental studies on distribution and abundance of animals in the field. In this

[1] This investigation was aided by a grant from the Commonwealth Research Grant to the University of Sydney.

paper it is shown how the magnitude of r may be influenced by temperature, moisture and food in the case of three grain beetles. All other components of the environment of these beetles have been kept constant, including the density of insects in the grain, which has been kept constant at an optimum in all experiments.

The effect of temperature and moisture on the innate capacity for increase r has been studied on the two beetles *Calandra oryzae* L. (small strain) and *Rhizopertha dominica* Fab. The study has covered the whole range of temperature and the greater part of the range of moisture within which these species can survive. The reason for the choice of species in this set of experiments is that *R. dominica* is typically a "tropical" species compared to *C. oryzae* which occurs in colder regions. It was hoped that this study might form a basis for understanding the different distribution and abundance of two such different species.

The effect of food (wheat and maize) on the intrinsic rate of natural increase has been studied on the two beetles *C. oryzae* (small strain) and *C. oryzae* (large strain) and at one combination of temperature (29.1°C) and relative humidity (70%). The two beetles are not inter-fertile and so they are really true sibling species though they have not yet been described as separate species (Birch 1944). The reason for choosing them in this experiment with different foods is that the small strain commonly occurs in stored wheat in Australia, but it has not been found in stored maize. On the other hand the large strain commonly occurs in maize but it has not been found in stored wheat. Yet both species breed in either wheat or maize in the laboratory. It was hoped that a study of the influence of food on their relative capacities for increase might throw some light on their distribution and abundance or at any rate serve as a basis for such studies. The temperature and moisture chosen for the experiments were within the optimum for the two beetles.

By means of studies on these three beetles I hope to show in this and subsequent papers how a knowledge of the innate capacity for increase and the way it is influenced by various components of the environment can contribute to an understanding of the distribution and abundance of animals.

The use of the intrinsic rate of natural increase in defining precisely tolerance ranges and therefore the limits to distribution of a species is dealt with in some detail. Only one aspect of its use in problems of abundance within the zone of tolerance is considered in this paper and that is when the only limiting factor to increase is the time available in which conditions are favourable for increase in numbers. The influence of crowding, both by the same and other species on the rate of increase is a consideration of subsequent papers. In those more complex conditions the index r may serve still as a valuable basis for study.

Experimental Procedure and Results

The insects used in all experiments were obtained from stock cultures which had been maintained for several months under constant conditions. Cultures of both strains of *C. oryzae* were kept at 29.1° C and 70% relative humidity in both wheat and maize; *R. dominica* was cultured at 32.3° C and 70% relative humidity in wheat. The temperature of experiments was controlled to ±0.1° C. Humidity was kept constant with saturated salt solutions and also with sulphuric acid solutions of appropriate concentration.

The intrinsic rate of natural increase of the three species under various experimental conditions has been determined from three sets of experimental data: the life table or l_x table, the duration of development of the immature stages and the age schedule of female births or m_x data. The life table gives the proportions of individuals alive at the beginning of arbitrarily chosen age intervals from birth to the death of the last individual in the population. The age schedule of fe-

male births is the number of female births (or eggs laid which would develop into females if they survived to maturity) for each parental age group such as one, two and three weeks of age. For any particular age group of pivotal age x, m_x is the number of female births. In the case of the insects used in these experiments m_x is the weekly number of eggs divided by two since only half the eggs are destined to become females. The insect is conveniently considered to be of zero age as a newly laid egg. The age of the newly emerged adult can therefore only be known when the duration of the immature stages of egg, larva, prepupa and pupa is known.

The procedure used for determining the life table and the age schedule of fecundity is given together with the results in the following subsections. The combination of these data to give the intrinsic rates of natural increase of the insects is given in the later section.

The Life Table

In estimating the intrinsic rate of natural increase over a wide range of temperature and humidity it was not necessary to determine the adult life table for every temperature and humidity studied. Preliminary estimates of r at different temperatures and humidities indicated that differences in the adult life tables made little difference to the value of r when the total mortality of the immature stages was greater than 50 per cent. It was necessary, of course, to determine the mortality of the immature stages under all combinations of temperature, moisture, and food for which values of r were required. This information is shown in columns three of Tables III, IV and V. Some of the data were obtained from Birch (1945a), the rest of the data were obtained by the same procedure described in this earlier paper. On the basis of these data on mortality of immature stages the following set of conditions was selected for determining the life tables of adults:

Species	*Temp.° C*	*Relative humidity*	*Grain*
C. oryzae (small strain)	29.1	70	Wheat
C. oryzae (small strain)	29.1	70	Maize
C. oryzae (small strain)	32.3	70	Wheat
C. oryzae (large strain)	29.1	70	Wheat
C. oryzae (large strain)	29.1	70	Maize
R. dominica	32.3	70	Wheat

A total of 800 newly emerged adults (0-15 hours old) was used in each experimental determination of a life table. The beetles were obtained from stock cultures which had been kept for several months at the same temperature and humidity and with the same food as in the experiment. Each lot of 800 adults was divided into 20 replicates of 40 insects, each in 12 grams of grain. This was equivalent to a density of one insect per 10 grains of wheat and one insect per 0.8 grains of maize. Because of the difficulty of sexing the living beetles no attempt was made to sex the beetles until after they had died in the experiment.

The insects and grain were kept in 4″ x 1″ glass tubes covered at the open end with phosphor-bronze gauze. These were kept in incubators at a constant temperature and humidity. The tubes were examined weekly for dead insects; these were then removed, sexed and counted. Throughout the experiment the population density in each tube was kept constant, so far as possible, by replacing dead insects with living ones from the highest-numbered tube, to bring the others back to a total of 40 insects per tube. Thus the number of tubes became reduced during the experiments but the density of insects remained reasonably constant. At two-weekly intervals the grain was completely replaced with new grain.

Since the beetles were not sexed at the beginning of the experiments the sexes were not represented by exactly the same numbers. The only serious inequality of numbers occured in the experiments with the small strain of *C. oryzae* in wheat and in maize where final analysis revealed about twice as many females as males. Previous workers on insect life tables

TABLE I. The mean length of life in weeks of adults of three grain beetles at 70% relative humidity.

Species	Temp. °C	Food	Male			Female		
			Mean	s.d.	C.V.	Mean	s.d.	C.V.
C. oryzae (Small Strain)	29.1	Wheat	16.58	7.27	44	17.05	6.86	40
C. oryzae (Small Strain)	29.1	Maize	28.93	11.14	39	23.18	7.85	34
C. oryzae (Small Strain)	32.3	Wheat	10.78	5.44	50	10.70	3.87	36
C. oryzae (Large Strain)	29.1	Wheat	19.63	7.73	39	18.13	7.23	40
C. oryzae (Large Strain)	29.1	Maize	25.22	10.83	43	18.33	8.37	46
R. dominica	32.3	Wheat	19.67	5.03	26	17.21	5.91	34

s.d.=standard deviation. C.V.=coefficient of variability.

have adopted the practice of keeping the sexes separate. This was not done in these experiments as we wished to know the length of life of the insects under the sorts of conditions existing in a laboratory culture. For the purposes of estimating r we are only interested in the life table of the female but the life table of the male has also been determined because of its general interest.

The mean length of life of adults is shown in Table I; the coefficients of variability are of the usual order for such data. Females had a greater longevity than males in four out of six experiments. In the remaining two experiments the longevity of the two sexes was about the same. These results are discussed below. The longevity of both strains of *C. oryzae* is greater in maize than in wheat with the exception of the female of the large strain which has about the same mean length of life in wheat and in maize. The relative increase in longevity in maize is greatest for males and is greatest for the male of the small strain which lives 12 weeks longer in maize; this is a surprisingly large increase.

The life tables are shown in Table II and in Figures 1 to 6 (complete lines).

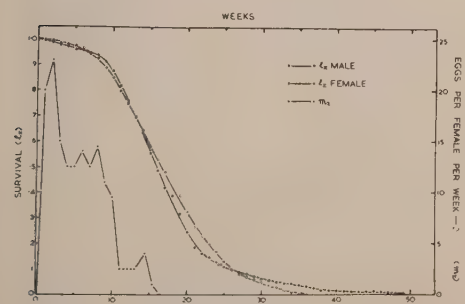

FIG. 1. The adult survival rate and the fecundity of the small strain of *Calandra oryzae* at 29.1° C in wheat of 14% moisture content. The l_x curves show the life tables of adults. The m_x curve shows the number of eggs laid per female per week ÷ 2.

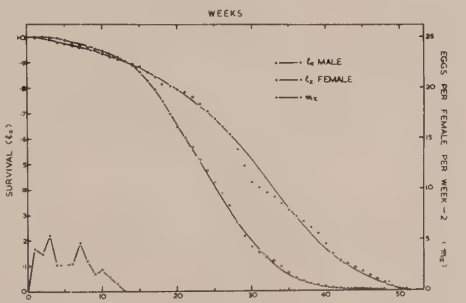

FIG. 2. The adult survival rate and the fecundity of the small strain of *Calandra oryzae* at 29.1° C in maize of 13% moisture content. The l_x curves show the life tables of adults. The m_x curve shows the number of eggs laid per female per week ÷ 2.

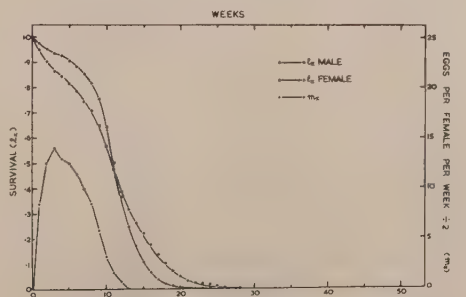

FIG. 3. The adult survival rate and the fecundity of the small strain of *Calandra oryzae* at 32.3° C in wheat of 14% moisture content. The l_x curves show the life tables of adults. The m_x curves show the number of eggs laid per female per week ÷ 2.

TABLE II. Life tables of adult grain beetles. The figures in the body of the table show the proportion of beetles alive (l_x) at the beginning of each age interval x. (See Figs. 1-6.)

Species	*C. oryzae* Small strain		*C. oryzae* Small strain		*C. oryzae* Small strain		*C. oryzae* Large strain		*C. oryzae* Large strain		*R. dominica*	
Temperature °C	29.1		29.1		32.3		29.1		29.1		32.3	
Humidity %	70		70		70		70		70		70	
Food	Wheat		Maize		Wheat		Wheat		Maize		Wheat	
No. of Insects	205	543	205	550	388	373	300	517	304	443	352	372
Age in Weeks	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
0 - 1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
1 - 2	.993	.996	.998	1.000	.950	.976	.995	1.000	.996	.995	1.000	.997
2 - 3	.987	.991	.995	1.000	.902	.954	.994	.999	.992	.988	1.000	.988
3 - 4	.975	.983	.987	.999	.864	.937	.988	.999	.983	.978	1.000	.978
4 - 5	.969	.978	.979	.996	.846	.926	.977	.992	.974	.968	.999	.969
5 - 6	.959	.971	.971	.987	.816	.905	.959	.983	.961	.954	.998	.966
6 - 7	.955	.961	.964	.976	.785	.882	.939	.970	.955	.938	.994	.958
7 - 8	.945	.942	.959	.965	.744	.853	.926	.959	.950	.914	.990	.949
8 - 9	.937	.921	.953	.958	.707	.819	.916	.940	.946	.891	.985	.935
9 - 10	.911	.887	.946	.953	.650	.754	.902	.918	.937	.866	.977	.922
10 - 11	.873	.848	.933	.946	.568	.644	.884	.890	.924	.839	.968	.906
11 - 12	.818	.797	.921	.936	.478	.504	.855	.851	.907	.807	.953	.879
12 - 13	.759	.748	.913	.922	.388	.365	.815	.799	.887	.771	.937	.837
13 - 14	.697	.692	.906	.905	.318	.248	.775	.750	.860	.733	.915	.778
14 - 15	.634	.644	.895	.887	.263	.170	.745	.694	.836	.688	.894	.707
15 - 16	.550	.579	.883	.861	.221	.108	.716	.639	.807	.634	.839	.624
16 - 17	.483	.529	.860	.830	.178	.068	.685	.578	.784	.583	.760	.545
17 - 18	.419	.478	.841	.793	.139	.037	.648	.523	.756	.536	.659	.477
18 - 19	.385	.440	.816	.747	.102	.020	.603	.467	.731	.498	.584	.434
19 - 20	.312	.385	.803	.695	.073	.013	.556	.403	.708	.447	.522	.391
20 - 21	.243	.324	.793	.646	.050	.009	.503	.342	.679	.402	.475	.351
21 - 22	.181	.265	.782	.602	.032	.005	.456	.293	.637	.349	.418	.301
22 - 23	.159	.226	.764	.564	.026	.004	.414	.260	.595	.307	.358	.254
23 - 24	.145	.197	.736	.518	.023	.003	.376	.235	.556	.266	.297	.196
24 - 25	.129	.169	.707	.472	.020	.002	.340	.212	.523	.235	.237	.150
25 - 26	.109	.129	.678	.427	.014	.001	.280	.185	.489	.203	.167	.097
26 - 27	.098	.097	.648	.382	.006	.000	.218	.160	.457	.172	.105	.060
27 - 28	.088	.078	.618	.336	.002	....	.162	.135	.425	.144	.054	.029
28 - 29	.080	.068	.553	.269	.000	....	.136	.109	.398	.126	.003	.015
29 - 30	.070	.059	.491	.215	....	....	.120	.088	.370	.105	.016	.010
30 - 31	.062	.049	.426	.171	....	....	.109	.071	.350	.088	.012	.005
31 - 32	.055	.038	.405	.152	....	....	.075	.059	.336	.071	.010	.003
32 - 33	.049	.028	.386	.133	....	....	.040	.045	.317	.063	.008	.001
33 - 34	.044	.018	.369	.116	....	....	.009	.032	.289	.058	.004	.000
34 - 35	.041	.010	.343	.094	....	....	.004	.024	.254	.051	.001	
35 - 36	.037	.003	.315	.070	....	....	.003	.020	.217	.042	.000	
36 - 37	.031	.000	.291	.048	....	....	.003	.015	.189	.033		
37 - 38	.023	....	.272	.037	....	....	.003	.010	.161	.027		
38 - 39	.017	....	.247	.029	....	....	.002	.005	.147	.020		
39 - 40	.013	....	.223	.020	....	....	.001	.003	.121	.014		
40 - 41	.012	....	.181	.013	....	....	.000	.001	.099	.008		
41 - 42	.010	....	.145	.010	....	....	....	.000	.071	.006		
42 - 43	.010	....	.115	.008	....	....	....	....	.057	.005		
43 - 44	.010	....	.101	.006	....	....	....	....	.041	.004		
44 - 45	.010	....	.088	.005	....	....	....	....	.032	.030		
45 - 46	.010	....	.072	.004	....	....	....	....	.024	.002		
46 - 47	.009	....	.059	.002	....	....	....	....	.018	.002		
47 - 48	.005	....	.044	.001	....	....	....	....	.011	.001		
48 - 49	.002	....	.029	.000	....	....	....	....	.004	.001		
49 - 50	.000	....	.015	....	....	....	....	....	.001	.000		
50 - 51	....	....	.005	....	....	....	....	....	.000			
51 - 52	....	....	.000									

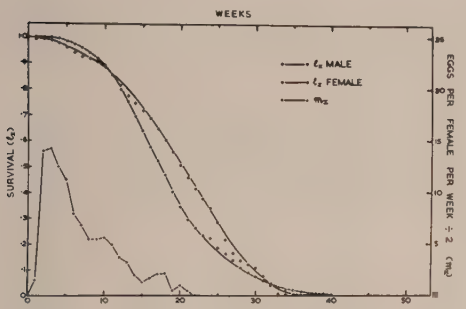

FIG. 4. The adult survival rate and the fecundity of the large strain of *Calandra oryzae* at 29.1° C in wheat of 14% moisture content. The l_x curves show the life tables of adults. The m_x curves show the number of eggs laid per female per week ÷ 2.

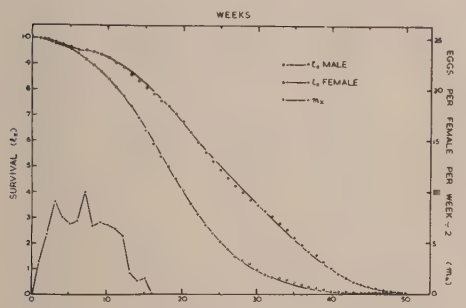

FIG. 5. The adult survival rate and the fecundity of the small strain of *Calandra oryzae* at 29.1° C in maize of 13% moisture content. The l_x curves show the life tables of adults. The m_x curves show the number of eggs laid per female per week ÷ 2.

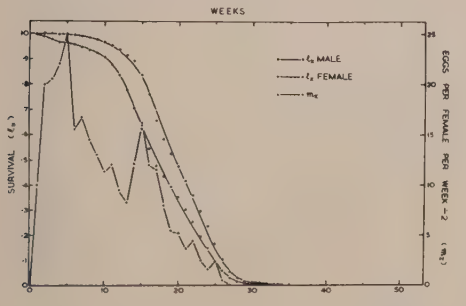

FIG. 6. The adult survival rate and the fecundity of *Rhizopertha dominica* at 32.3° C in wheat of 14% moisture content. The l_x curves show the life tables of adults. The m_x curves show the number of eggs laid per female per week ÷ 2.

They were constructed from the weekly records of deaths of males and females. Weekly survival is represented as a fraction of unity, hence survival at birth is represented by 1 and zero survival by 0. The data were smoothed by obtaining three weekly moving averages. It is these values which are shown in the tables and figures. Free-hand curves have been drawn through the plotted points but the three-weekly moving averages were used in the subsequent calculation of r. There seemed to be no particular merit in fitting mathematical expressions to the life tables and so this was not done.

Figures 1 to 6 show that the death rate of the adult was initially low in all experiments. It reached a maximum about the middle of the life span and decreased again towards the end of the life span. This is quite typical of a number of life tables of animals (c.f. Deevey 1947). In contrast *Tribolium confusum* (Pearl, Park, and Miner 1941) and the black widow spider (Deevey and Deevey 1945) are characterized by heavy mortality in the early life of the adult.

Age-specific Fecundity Rates

The number of eggs laid per female during each week of life has been determined for each combination of temperature and moisture shown in Tables III, IV, and V. The way in which this information was obtained has been described by Birch (1945b). It is only necessary to add that the fecundity of *C. oryzae* was determined at a density of one insect per ten grains of wheat and one insect per fifteen grains of maize. Ten pairs of insects were used in each experiment. With *R. dominica* twenty-five pairs were used at a density of one insect in four grains. Since fecundity was not very much greater at densities lower than these (Birch 1945b) we can safely assume that the rates correspond reasonably closely with those at the optimum density.

The age-specific fecundity rates for the six sets of conditions under which life tables were also obtained are shown in Figures 1-6. The data for the remaining experiments are not shown in detail since

TABLE III. Showing the effect of temperature and moisture on the innate capacity of the small strain of *C. oryzae* to increase in numbers in wheat. (Data in last column shown in Fig 8.)

Temp. °C	Percent moisture content of wheat	Percent[1] mortality immature stages	Total[2] number of eggs laid per female	Duration[3] of development egg to adult (weeks)	Mean length of a generation in weeks (T)	Rate of multiplication per generation (R_o)	Intrinsic rate of natural increase (r)		Finite rate of increase per female per week (λ)
							Approximate estimate	Accurate estimate	
13.0	14	100	0	...	...	0	$-\infty$	$-\infty$	0
15.2	14	75	1/week	32.9	39.2	1.23	0.005	0.005	1.007
18.2	14	12	4/week	15.5	20.4	17.32	0.133	0.140	1.15
23.0	14	10	266	6.1[5]	10.6	96.58	0.360	0.430	1.54
25.5	14	7	384	4.9	7.6	101.30	0.500	0.605	1.83
29.1	14	10	344	4.0	6.4	134.18	0.560	0.772	2.15
32.3	14	65	197	4.1	6.9	31.38	0.424	0.501	1.65
33.5	14	75	27	9.4	10.4	3.38	0.120	0.120	1.13
34.0	14	97	..	...	...	.....	.....	.....	....
35.0	14	100	5	...	...	0	$-\infty$	$-\infty$	0
15.2	12	100	0	...	...	0	$-\infty$	$-\infty$	0
23.0	12	40[4]	80	5.7	9.9	20.31	0.280	0.303	1.35
29.1	12	36[4]	75	4.3	7.5	20.79	0.349	0.406	1.50
33.5	12	88	20	9.4	10.7	1.14	0.001	0.001	1.00
34.0	12	100	0	...	0	0	$-\infty$	$-\infty$	0
15.2	11	100	0	...	...	0	$-\infty$	$-\infty$	0
18.2	11	86	21	16.1	19.5	1.30	0.013	0.013	1.10
25.5	11	64	72	5.2	8.5	13.81	0.279	0.310	1.36
29.1	11	38	66	4.4	8.3	17.98	0.310	0.350	1.42
33.5	11	97	0	...	...	0	$-\infty$	$-\infty$	0
18.2	10.5	99	0	...	...	0	$-\infty$	$-\infty$	0
25.5	10.5	88	16	5.7	8.6	1.77	0.067	0.067	1.07
29.1	10.5	76	10	4.3	7.1	0.75	−0.041	−0.041	0.96
32.3	10.5	100	..	...	...	0	$-\infty$	$-\infty$	0
15-35	10.0	100	..	...	...	0	$-\infty$	$-\infty$	0

[1]Data from Birch (1945a). [2]Data from Birch (1945b). [3]Data from Birch (1945c).
[4]Interpolated from Birch (1945d). [5]Interpolated from Birch (1945c).

they are extensive and of little interest except as a step in the estimation of *r*. Instead the total number of eggs is shown in column 4 of Tables III, IV, and V.

From Figures 1-6 (especially Figs. 2 and 5) and the data summarised in Table VI, it would appear that the last egg was always laid long before the last female died. But the l_x and m_x curves may not be compared in this way because the former are based on samples of 400 insects and the latter on samples of 10 female *Calandra* and 25 female *Rhizopertha*. The larger sample, by virtue of its size alone, is more likely to include long-lived individuals.

The Innate Capacity for Increase

In order to calculate the innate capacity for increase *r* it is necessary to know: (a) the life-table, (b) the duration of development of the immature stages, (c) the age specific fecundity rates. These data are not given in full for all the conditions of temperature and humidity studied because that would be cumbersome. Complete information is given for six examples; these are shown in Figures 1-6 and Tables III, IV, and V. The rest of the data given in Tables III, IV, and V are sufficient to indicate how the components of *r* vary with temperature, moisture and food.

A number of useful indices besides *r* have been calculated from these data. Methods of estimation have been given in full by Birch (1948) and these are repeated in outline below:

The intrinsic rate of natural increase *r*,

TABLE IV. Showing the effect of temperature and moisture on the innate capacity of *R. dominica* to increase in numbers in wheat. (Data in last column shown in Fig. 8.)

Temp. °C	Percent moisture content of wheat	Percent[1] mortality immature stages in sound grain	Total[2] number of eggs laid per female	Duration[3] of development egg to adult (weeks)	Mean length of a generation in weeks (T)	Rate of multiplication per generation (R_o)	Intrinsic rate of natural increase (r)		Finite rate of increase per female per week (λ)
							Approximate estimate	Accurate estimate	
18.3	14	100	38+	...	...	0	$-\infty$	$-\infty$	0
29.0	14	26	288[4]	4.6	7.6	97.05	0.439	0.578	1.78
32.3	14	21[4]	573[5]	4.0	7.0	123.39	0.517	0.686	1.99
34.0	14	22	415	3.5	6.5	141.69	0.562	0.762	2.14
38.2	14	86	97	5.2	7.1	8.04	0.288	0.294	1.34
38.6	14	100	...	...	...	0	$-\infty$	$-\infty$	0
18.3	11	100	45	...	...	0	$-\infty$	$-\infty$	0
22.0	11	89	181	13.4	19.6	7.83	0.120	0.105	1.11
38.2	11	91	113	6.6	8.7	4.55	0.174	0.174	1.19
38.6	11	100	...	...	...	0	$-\infty$	$-\infty$	0
22.0	10	100	132	13.4	...	0	$-\infty$	$-\infty$	0
26.0	10	85	256	5.1	12.0	18.58	0.216	0.243	1.28
34.0	10	77	295	5.0	8.9	30.00	0.334	0.383	1.47
36.0	10	88	172	5.6	9.6	12.15	0.238	0.261	1.30
38.2	10	100	52	6.6	...	0	$-\infty$	$-\infty$	0
30.0	9	100	...	...	...	0	$-\infty$	$-\infty$	0
34.0	9	98	315	5.0	8.7	16.38	0.280	0.321	1.38
36.0	9	100	160	5.6	...	0	$-\infty$	$-\infty$	0
18-38	8	100	...	...	...	0	$-\infty$	$-\infty$	0

[1]Data from Birch (1945a). [2]Data from Birch (1945b) except 29.1° and 32.3°C at 14 p.c. moisture content.
[3]Data from Birch (1945c). [4]Interpolated from Birch (1945d). [5]Additional experimental estimate.

TABLE V. Showing the effect of food (wheat and maize) on the innate capacity for increase of the small and large strains of *C. oryzae* at 29.1° C and 70% relative humidity. At this humidity wheat had a moisture content of 14% and maize had a moisture content of 13%.

Strain	Food	Percent mortality immature stages in grain	Total number of eggs per female	Duration of development, egg to adult (weeks)	Mean length of a generation in weeks (T)	Rate of multiplication per generation (R_o)	Mean duration of life of adult female in weeks	Intrinsic rate of natural increase (r)		Finite rate of increase per female per week (λ)
								Approximate estimate	Accurate estimate	
Small	Wheat	10	344[1]	4.0	6.4	134.18	17.05	0.560	0.772	2.15
Small	Maize	13	70	5.0	8.2	30.53	23.18	0.348	0.417	1.52
Large	Wheat	10	208[1]	4.4	8.0	89.43	18.13	0.436	0.564	1.76
Large	Maize	34.6	154	4.9	8.8	46.71	18.33	0.359	0.436	1.55

[1]Segrove (1951) records a higher total fecundity of the large strain compared with the small strain in England in wheat at 25°C and 70 % relative humidity.

(Columns 8 and 9, Tables III and IV; Columns 9 and 10, Table V):

An accurate estimate of r was obtained from the following relationship:

$$\int_0^\infty e^{-rx} l_x m_x dx = 1$$

TABLE VI. The relation between length of life of females and the ages at which 50% and 100% of eggs were laid.

Species	Temp. °C	Food	Percentage of females alive in the longevity experiments	
			At age when 50 p.c. of eggs had been laid in fecundity experiment	At age when last egg had been laid in fecundity experiment
C. oryzae (small strain)	29.1	Wheat	98	64
C. oryzae (small strain)	29.1	Maize	99	94
C. oryzae (small strain)	32.3	Wheat	93	37
C. oryzae (large strain)	29.1	Wheat	99	29
C. oryzae (large strain)	29.1	Maize	95	69
R. dominica	32.3	Wheat	94	15

where l_x is the proportion of individuals alive at the beginning of the age interval x and m_x is the number of female births for the particular age group of pivotal age x.

An approximate short-cut estimate of r (see Birch 1948) is also shown in Tables III, IV, and V but this method is only of sufficient accuracy when r has a low value not exceeding about 0.200 (see Columns 8 and 9, Tables III and IV; Columns 9 and 10, Table V).

The finite rate of increase per female per week (λ), (last column, Tables III, IV, and V):

The finite rate of increase is the multiplication per female per week which a population of stable age distribution would have when increasing in a constant environment in which space was unlimited. λ is derived from the intrinsic rate of increase r by the following relationship:

$$\lambda = \text{antilog}_e r.$$

We shall use λ as our expression of the innate capacity for increase rather than r since it is an easier concept for the non-mathematical ecologist to grasp. A ready conversion of r to λ covering the values given in Tables III, IV, and V is given in Figure 7.

The multiplication per generation (R_o), (Column 7, Tables III, IV, and V):

$$R_o = \Sigma\, l_x\, m_x$$

The mean length of a generation (T), (Column 6, Tables III, IV, and V).

$$T = \frac{\log_e R_o}{r}$$

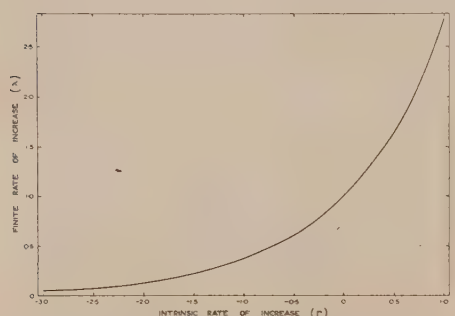

FIG. 7. The relationship between the intrinsic rate of natural increase r and the finite rate of natural increase λ. ($\lambda = \text{antilog}_e\, r$)

The effect of temperature and moisture on the finite rate of increase of the small strain of C. oryzae *and* R. dominica.

The finite rates of increase (λ) of *C. oryzae* and *R. dominica* which are shown in the final columns of Tables III and IV have been plotted in Figure 8. The points on the graph indicate the combinations of temperature and moisture for which values of λ have been obtained. To avoid confusion the actual values of λ at these points are not shown but isopleths have been drawn through points of equal value of λ. The lines show the way in which temperature and moisture differentially affect the innate capacity for increase of the two species.

For each species there is a particular zone of temperature and moisture within which the capacity for increase is great-

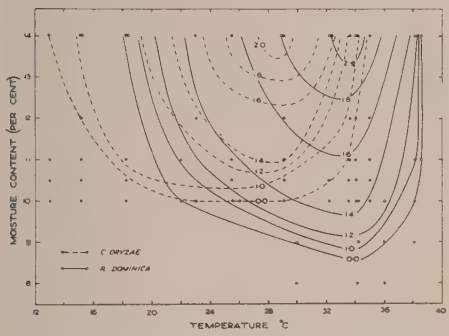

FIG. 8. The finite rate of increase (λ) of *Calandra oryzae* (small strain) and *Rhizopertha dominica* living in wheat of different moisutre contents and at different temperatures. (See final columns of Tables III and IV.)

est. This is the zone within the isopleth $\lambda = 2$. There is also a zone beyond which no increase can occur at all: this is defined by the isopleth $\lambda = 1$ ($r = 0$). When $\lambda = 1$ the species cannot increase but it could maintain its numbers from generation to generation. The isopeth for $\lambda = 0$ ($r = -\infty$) defines the zone in which no insects of reproductive age would be added to the population because the death rate of immature stages is 100%. Between the zero isopleth and the isopleth for unity (r is negative) the death rate exceeds the birth rate and although some eggs are laid the death rate is so high that the population eventually dies out. The rate at which it dwindles is directly proportional to the value of λ.

Some indication of the relative importance of birth rate and death rate in determining any particular value of λ in these experiments can be gained from a glance at the columns for total fecundity (column 4) and death rate (column 3) in Tables III and IV. For example, *R. dominica* invariably continued to lay some eggs under conditions in which none of the eggs survived. This is true of *C. oryzae* at some temperatures in wheat of 14% moisture content, but in drier wheat a temperature which caused 100% mortality in the immature stages also prevented adults from laying any eggs.

Various deductions can be made from Figure 8 about the possible distribution and abundance of the two species. It is clear that *R. dominica* can invade drier and hotter wheat than can *C. oryzae*. On the other hand *C. oryzae* can increase in numbers in wheat which is so cold that *R. dominica* cannot survive. The relative geographic distribution of the two species will therefore be related to the relative positions of the zero boundaries in Figure 8.

The known distribution of the two species in nature confirms these deductions. For example *R. dominica* is virtually absent from the coldest state of Australia (Tasmania) whereas *C. oryzae* is quite common there. *R. dominica,* on the other hand has been known to become a serious pest in the warmer mainland when wheat was stored for periods of a year or more (Wilson 1945).

The area within the isopleth $\lambda = 1$ (Fig. 8) defines the zones of temperature and moisture which are tolerable for survival of populations of these insects. Theoretically numbers could increase indefinitely at any combination of temperature and moisture within this boundary provided other factors of the environment were not limiting. But the rate at which numbers increased within this zone would vary tremendously depending upon the particular value of λ. It would be fastest when λ was a maximum.

The effect of temperature and moisture

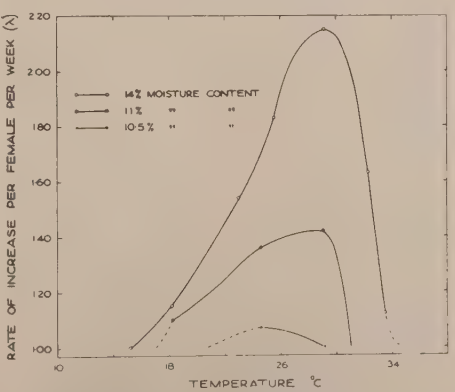

FIG. 9. The finite rate of increase (λ) of *Calandra oryzae* living in wheat of different moisture contents and at different temperatures. (See final columns of Table III.)

on the innate capacity for increase of *C. oryzae* in the tolerable zone is shown in Figure 9. In wheat of 14% moisture content there is a curvilinear relationship between temperature and the innate capacity for increase, the curve drops sharply after it reaches a peak. The theoretical number of individuals at the end of n weeks is given by λ^n. For example, at 15.2° C one female would give rise to $(1.007)^{10} = 2$ females and 2 males. In the same time at 29.1° C one female would give rise to $(2.15)^{10} = 2014$ females and the same number of males. In other words in 10 weeks at 29.1° C the population would be 2000 times greater than it would be in the same time at 15.2° C.

Similar comparisons might be made between the two species in the same environment. Figure 8 shows that in wheat of 14% moisture content *C. oryzae* has a greater innate capacity for increase than *R. dominica* at all temperatures up to 31° C. At 31° C the value of λ is the same for both species ($\lambda = 1.8$), but at temperatures higher than 31° C *R. dominica* has a greater innate capacity for increase than *C. oryzae*. As the moisture content of wheat drops *R. dominica* gains the ascendency at lower temperatures. This is shown in Figure 8 by the way in which the intersections of isopleths for the same value of λ are further to the left at the lower moisture contents. This information is summarised in Table VII which shows the combinations of temperature and moisture at which the isopleths for values of λ from 1 to 1.8 intersect in Figure 8.

The importance of small differences in temperature on the relative rates of increase of populations of the two species is illustrated in the following examples for insects living in wheat of 14% moisture content:

In 10 weeks at 29.1° C one female of *R. dominica* gives rise to $(1.78)^{10} =$ 319 females.

In 10 weeks at 29.1° C one female of *C. oryzae* gives rise to $(2.14)^{10} =$ 2014 females.

TABLE VII. Showing combinations of temperature and moisture at which *R. dominica* and the small strain of *C. oryzae* have the same innate capacity for increase (λ). (See Fig. 8).

Finite rate of increase (λ)	Temp. °C	Moisture content % of wheat
1.8	30.0	10.3
1.6	28.3	12.0
1.4	24.5	11.7
1.2	21.5	12.8
1.0	23.5	13.0

In 10 weeks at 32.3° C one female of *R. dominica* gives rise to $(2.0)^{10} =$ 1024 females.

In 10 weeks at 32.3° C one female of *C. oryzae* gives rise to $(1.65)^{10} =$ 150 females.

In these examples an increase of 3.2° C causes a threefold increase in numbers of *R. dominica* but a 13-fold decrease in numbers of *C. oryzae*.

We have discussed the way in which the innate capacity for increase varies for the two species within the zone of tolerance (*i.e.*, where λ exceeds unity). Species do not, of course, go on increasing indefinitely in nature at these rates. This does not necessarily mean that this information is of little use as a guide to possible abundance of different species in nature. Its possible application can be illustrated by a hypothetical model. We might imagine a situation in which food and space were relatively unlimited but the time during which temperature, moisture and other factors were favourable for increase (*i.e.*, λ exceeded 1) was limited to a short period in each year. During this favourable period a species which had a high value of λ would reach higher numbers than one which had a low value of λ. It would be called a common species by comparison. In this simplified model we would expect presence and absence of a species to be related to its innate capacity for increase and within its range of tolerance commonness and rareness would be related to the innate capacity for increase. This model is, of course, an abstraction from nature. There, all sorts of factors

operate together to determine abundance. But it may nevertheless represent one important aspect of what happens in some natural populations.[1]

The effect of food on the finite rate of increase of the small and large strains of C. oryzae.

The small and large strains of *C. oryzae* both breed readily in maize as well as in wheat in laboratory cultures, although the small strain appears to be confined to wheat and the large strain confined to maize in field stores of grain. It would seem that the type of food has some influence on distribution and abundance. The innate capacity for increase of the two species in both sorts of grain has therefore been determined as basic data for studying this problem.

The information necessary for the estimation of r (and λ) was obtained for both beetles in wheat and maize at 29.1° C at a relative humidity of 70%. At this humidity wheat had a moisture content of 14% and maize had a moisture content of 13%. There was thus a difference in moisture content of the two sorts of grain as well as a difference in quality. The method of obtaining the information for the estimation of r(and λ) was the same as that already described. The results are shown in Figures 1, 2, 4 and 5, and in Table V. The last column of the table shows the innate capacity for increase expressed as the finite rate of increase λ.

The small strain has a much higher innate capacity for increase in wheat than in maize. The large strain has also a higher innate capacity for increase in wheat compared with maize but the difference is much smaller. Comparison of the two beetles in the same sort of grain shows that the small strain has a higher innate capacity for increase than the large strain in wheat. But in maize the reverse is true; the large strain has a higher innate capacity for increase than the small strain. In other words, under the conditions of these experiments, maize favours the large strain and wheat favours the small strain. We would, of course, need much more information than this from which to draw any conclusions about distribution and abundance, but this much information does suggest that at a favourable temperature and humidity the large strain would have an initial advantage over the small strain in maize and vice versa in wheat. Other factors may also work in the direction of favouring the small strain in wheat and the large strain in maize and some of these are being investigated.

Since Table V and Figures 1, 2, 4 and 5 give the components of birth rate and death rate which determine the values of λ, they can be used to indicate which components of the innate capacity for increase are largely responsible for the differences in λ shown in the last column of Table V. For example, the reduction of λ for the small strain in maize as compared with wheat is primarily due to a tremendous reduction in the number of eggs laid in maize (Figs. 1 and 2, Table V column 4), and the slower development of the immature stages in maize (Table V column 5). The mortality of the immature stages is about the same in both grains but it is surprising to find that the length of life of adults is greater in maize than in wheat (Table V column 8).

We have already pointed out that the reduction in the value of λ for the small strain in maize compared with wheat is greater than the corresponding comparison for the large strain. This is primarily due to the greater reduction of fecundity of the small strain in maize. The reduction in fecundity of the large strain in maize is so much less that the large strain has a higher value of λ despite its higher mortality.

These differences of the innate capacities of the two strains in wheat and maize are recorded in the absence of any additional data which might explain them. The reduction of fecundity in maize is possibly due to its greater hardness and the difficulty of boring oviposition holes

[1] Since writing this a nice example has been provided by Howe (1953).

into the hard surface. But this possibility has not yet been investigated.

Acknowledgments

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Conclusion and Summary

Although numerous studies have been made on the various components of birth rate and death rate of insects and other animals, this appears to be the first in which all the components of birth rate and death rate necessary for the estimation of the innate capacity for increase have been determined over the complete range of temperature tolerable and over a wide range of moisture. Data are given on the precise effect of temperature and moisture on the innate capacity for increase of the small strain of *C. oryzae* and *R. dominica* at an optimum density of insects in wheat. Data are also provided on the effect of wheat and maize on the innate capacity for increase of the large and small strains of *C. oryzae*.

The significance of this information is that it provides background experimental data for studies on distribution and abundance.

The limits of distribution of the beetles are determined, so far as temperature and moisture are concerned, by the combinations of temperature and moisture beyond which the finite rate of increase (λ) is less than 1 (the intrinsic rate of increase r is negative).

Within the zone of temperature and moisture tolerable for the insects, their abundance, under certain circumstances, may be related to the innate capacity for increase (expressed either as λ or r.). Only certain aspects of this larger problem are considered in this paper, in particular the relationship between λ and abundance when the limiting factor for increase is the length of time during which conditions are favourable for increase (*i.e.*, when λ is greater than 1). When time is the only limiting factor then we would expect to find a relationship between abundance and the value of λ. Other factors such as crowding, parasites and competitors are a further complication; some of these factors are considered in a forthcoming paper.

Data on the innate capacity for increase of *C. oryzae* and *R. dominica* show that the temperatures tolerable for increase are lower for *C. oryzae* than *R. dominica*. *R. dominica* can also tolerate drier wheat. This corresponds with the known distribution of these species in Australia.

The two strains of *C. oryzae* can breed in wheat and in maize in the laboratory, but the large strain has only been found in maize and the small strain has only been found in wheat in stores in the field. At a favourable temperature and humidity (29.1° C and 70% relative humidity) in the laboratory, the innate capacity for increase of the small strain is greater than that of the large strain. But the reverse is true in maize. This may be one of a number of factors which combine to make the small strain common in wheat and the large strain common in maize.

From tables showing birth rates (age-specific fecundity rates) and death rates (the adult life table and mortality rates of immature stages) it can be seen how temperature, moisture and food influence the components of the innate capacity for increase. The combinations of temperature and moisture which result in a drastic reduction in birth rate also cause a drastic increase in death rate. The influence of food appears to be different. Maize causes a great reduction in birth rate compared with wheat in both strains of *C. oryzae* but the increase in the death rate is quite small for the small strain though appreciable for the large strain. The combined effect is that the small strain has a much higher innate capacity for increase in wheat than in maize. The large strain has a slightly higher innate

capacity for increase in wheat as compared with maize.

Some data additional to that necessary for the estimation of the innate capacity for increase have been provided in this paper. The complete life tables of adult males and females were determined under six different sets of conditions, although only the life table of the female during her egg laying life is required for the estimation of λ. In four out of six experiments males had a greater longevity than females. This result contrasts with previous studies on longevity of other insects where males have been shown to have a shorter life than females (*e.g.,* Deevey 1947; Pearl, Park, and Miner 1941). But in these latter experiments males and females were kept separately. In the experiments described in this paper they were kept together and under these circumstances females lay many more eggs than do virgin females. It is possible that the extra drain on the resources imposed by egg-laying shortens the life of the female compared to what it would be for a virgin female.

The longevity of the small strain of *C. oryzae* was much greater in maize than in wheat. The same was true of males of the large strain. But there was little difference in longevity of females of the large strain in wheat and maize.

Whereas longevity was increased in maize the fecundity of the small and large strains of *C. oryzae* was very much less in maize than in wheat. This is possibly due to the greater hardness of maize and the consequent difficulty in boring oviposition holes. Comparison of the life table and the fecundity table suggests that a large proportion of females lived for weeks after they would have laid their last eggs. This result may, however, be an artifact since smaller numbers of insects were used in obtaining the age-fecundity data compared with large numbers used in obtaining the life table.

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EXPERIMENTAL BACKGROUND TO THE STUDY OF THE DISTRIBUTION AND ABUNDANCE OF INSECTS

II. THE RELATION BETWEEN INNATE CAPACITY FOR INCREASE IN NUMBERS AND THE ABUNDANCE OF THREE GRAIN BEETLES IN EXPERIMENTAL POPULATIONS[1]

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Introduction

The effect of temperature, moisture and food on the innate capacity for increase in numbers of the three grain beetles *Rhizopertha dominica,* the small and the large forms of *Calandra oryzae* was described in a previous paper (Birch 1953). The innate capacity for increase was defined as the intrinsic rate of increase r or its expression as a finite rate λ, where $\lambda = \text{antilog}_e r$. This is the rate of increase of a population of stable age distribution growing in unlimited space at its optimum density. Sometimes it is more convenient to express the innate capacity for increase as a finite rate and at other times the infinitesimal rate of increase is a more convenient mode of expression. One purpose of this previous contribution was to show how some of the problems of distribution and abundance might be more adequately studied if we had experimental knowledge of the effect of environmental factors such as temperature, on the animal's capacity to increase in numbers. This information for three grain beetles was discussed in relation to a hypothetical model of a population growing in unlimited space, but in which the time during which conditions were favourable for increase was the factor limiting the numbers of animals in the population.

In the experimental models described in this paper, populations of the same three beetles were grown in a limited space and food was regularly replenished to a constant amount so that as far as possible a constant quantity of food was available to the population. All other components of the environment such as temperature and moisture were kept constant for any one experimental model. Models such as these are commonly set up by ecologists and geneticists in their investigation of animal populations. We wished to investigate whether the innate capacity for increase (r) might be a useful index in analysing the growth and abundance of insects in populations maintained under these carefully controlled conditions.

Although the conditions in experimental models are far removed from populations in nature they may nevertheless provide some clues to the problems of distribution and abundance which might not otherwise be recognised. They might also possess an ancillary value for the population geneticist who works with similar models in his laboratory experiments. He is, of course, primarily interested in the qualitative changes in his populations but in interpreting these changes he may need to know something about the factors which influence numbers.

The experiments described in this paper were done with the additional objective of establishing information necessary for another series of experiments on the effects of one species on the rate of increase of another when both species occurred together in the same space.

Procedure

Each experimental model consisted initially of a single pair of newly emerged beetles (up to 12 hours old) in 12 grams of grain. Wheat of 14% moisture content was used in some experiments and maize of 13% moisture content was used in others. The grain was conditioned at

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70% relative humidity over saturated solutions of sodium chloride. The grain with the insects was kept in 4" x 1" vials with phosphor bronze gauze coverings at one end. They were kept upside down in incubators at constant temperatures and at constant humidities. This was necessary for otherwise the grain increased in moisture content and became mouldy as the populations grew; the circulation of air was much better in vials kept upside down. Experiments were done at two temperatures 29.1° C±0.1° C and 32.3° C ±0.1° C. Humidity was kept at about 70% relative humidity with trays of saturated solutions of sodium chloride onto which a fan played.

The grain and insects were sifted every two weeks for the duration of the experiments, flour and frass were removed, the grain was made up to 12 grams. Adults were counted every two weeks for the first 8 weeks and then at monthly intervals. The details of the sifting were slightly different for populations of *Rhizopertha* as compared with those of *Calandra*. Flour tends to accumulate in cultures of *Rhizopertha;* this was sifted off, leaving the insects with grain in various degrees of subdivision, some of it being in quite small fragments. Little flour was formed in the *Calandra* cultures, but empty husks tend to accumulate in between siftings. These were blown off, otherwise husks would eventually take up all the space in the vials. The routine in either case was designed to keep the quantity and quality of food constant.

Seven different experimental models were set up and each was replicated 15 times (Table I). Counts of adults were continued in most of the experiments for two years and in one set of experiments for nearly four years.

Two considerations weighed in the choice of species, temperature, moisture and food for the experiments. In the first place I wished to have a series of populations which differed considerably in their innate capacity for increase, *r*. This information had been determined previously (Birch 1953) and is shown in Table I. Secondly the experiments were also designed to served as "control" experiments for another series of experiments to be described elsewhere in which two species were together in the same vials feeding on the same food.

The Trend in Numbers

The trend in numbers of adults in the seven series of experiments is shown in Figures 1-4. Pairs of experiments on the one graph are those which we are particularly interested in comparing. Each point on the graphs is the mean of 15 replicates. There was fortunately a surprisingly good agreement between replicates so that the means shown are reliable estimates. The complete data for all experiments are so extensive that these tables are not given. Instead a summary of the variability is provided in Table II. The coefficients of variability of some 180 means were calculated. These were then arranged in groups of four. The means of these four values are shown in Table II. This grouping is sufficiently fine to re-

Table I. Showing the seven series of experiments in which populations were grown with a constant amount of grain.

Species	Grain	Moisture Content %	Temp. °C	Innate capacity for increase	
				r	λ
C. oryzae (small strain)	Maize	13	29.1	0.417	1.52
C. oryzae (large strain)	Maize	13	29.1	0.436	1.55
C. oryzae (small strain)	Wheat	14	29.1	0.772	2.15
C. oryzae (large strain)	Wheat	14	29.1	0.564	1.76
R. dominica	Wheat	14	29.1	0.578	1.78
R. dominica	Wheat	14	32.3	0.686	1.99
C. oryzae (small strain)	Wheat	14	32.3	0.501	1.65

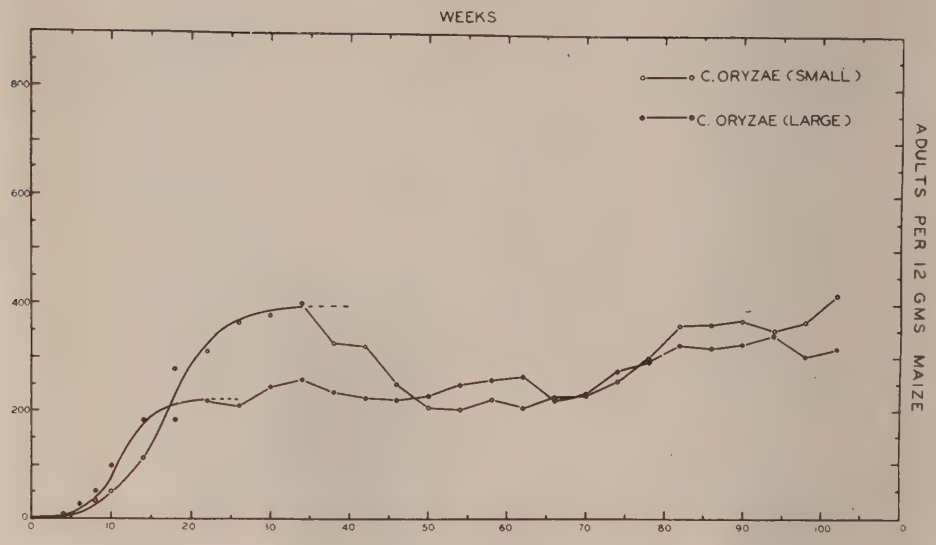

FIG. 1. The trend in numbers of adults of the small and the large strains of *C. oryzae* in separate populations in maize of 13% moisture content at 29.1° C. The smooth curves are calculated logistic curves. (See Table III.)

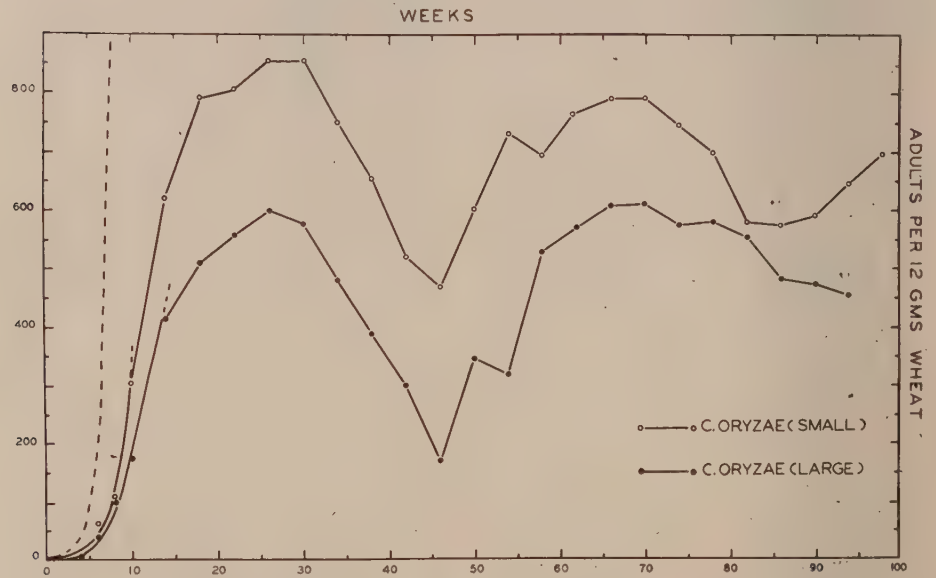

FIG. 2. The trend in numbers of adults of the small and the large strains of *C. oryzae* in separate populations in wheat of 14% moisture content at 29.1° C. The smooth curves are calculated logistic curves. (See Table III.) The broken line on the left of the diagram shows the estimated geometric increase of the small strain when $r = 0.772$.

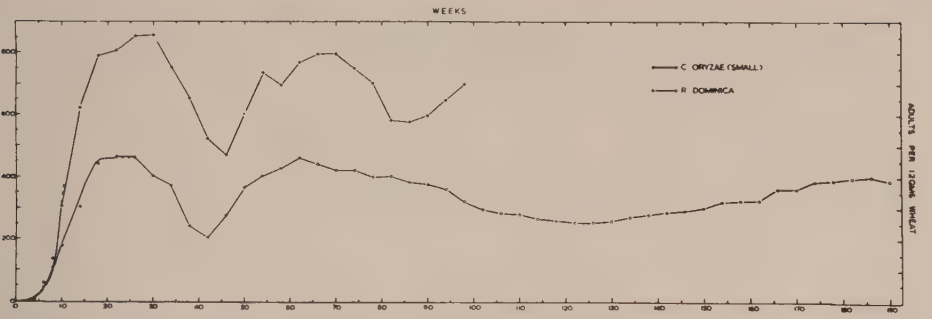

FIG. 3. The trend in numbers of adults of the small strain of *C. oryzae* and *R. dominica* in separate populations in wheat of 14% moisture content at 29.1° C. The smooth curves are calculated logistic curves. (See Table III.)

flect the trend in variability with time. When all the values for the coefficient of variability were plotted against time they showed oscillations which were just the reverse of those shown by the means plotted in Figures 1-4; the peaks of variability coincided with minimum numbers and the minimum variability coincided with maximum numbers.

The initial trend in numbers of each population was sigmoid. This was followed by long-term oscillations. Logistic curves were fitted to the first phase of population growth where density was increasing continuously. Since there were no asymptotes in any of the population trends, a hypothetical asymptote was chosen in calculating the curve such that the ensuing curve gave the best fit for the greatest part of the data relating to the first phase of growth when density was increasing continuously. The calculated curve covered the full span of this phase of growth in four of the seven experiments (see Figs. 1, 3 and 4). But in the remaining cases it was not possible to obtain a curve to fit any more than a small segment of the initial trend. Calculated curves are shown as smooth lines in the figures; theoretical extrapolation of the curves beyond the points on which they were based are shown as broken lines. Formulae of the curves are given in Table III.

Four of the experiments were terminated at the 100th week and one was continued for 190 weeks (Fig. 3). During this time one and a half oscillations were completed. Experiments shown in Figure 4 were terminated at the 50th week before one full oscillation was completed; however, populations of these two species were maintained for several years under similar conditions though records of their numbers were not kept.

The Relation Between Innate Capacity for Increase and Population Maxima

The densities about which numbers oscillate in Figures 1-4 vary for each experiment. In Figure 2, for example, the density of the large strain of *C. oryzae* never gets as high as the maximum density of the small strain, nor does the density of the small strain get as low as that of the large strain in the valleys of the oscillations. Rather than compare the mean densities about which numbers appear to oscillate it seems more realistic to compare the maximum numbers reached in the populations, because this has a reality which the mean does not possess. There is, of course, the disadvantage that the estimate of maximum numbers is based on the mean of 15 replicates at only two stages of the history of the population (Figs. 1-3) and at only one stage of its history for the two populations shown in Figure 4.

The relationship between mean maximum numbers and the innate capacity for increase is shown in Figure 5A. For the small and the large strains of *C.*

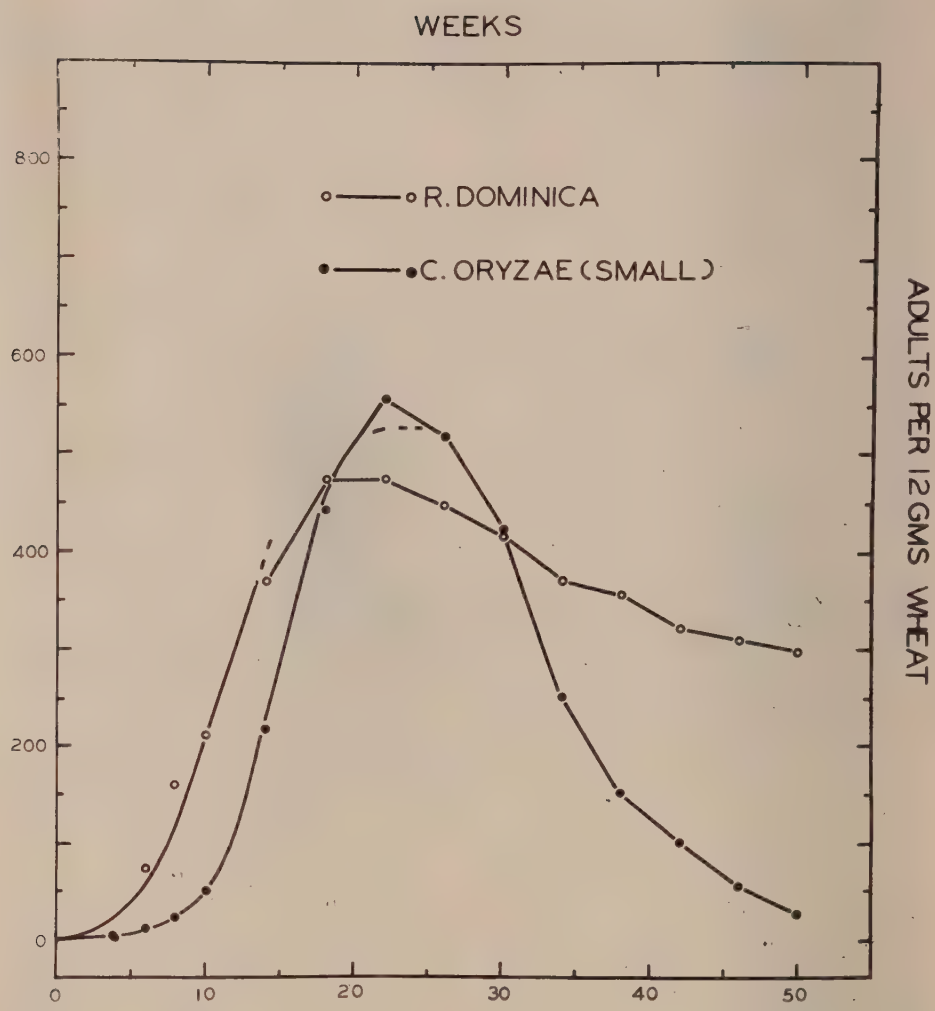

FIG. 4. The trends in numbers of adults of the small strain of *C. oryzae* and *R. dominica* in separate populations in wheat of 14% moisture content at 32.3° C. The smooth curves are calculated logistic curves. (See Table III.)

oryzae the greater the innate capacity for increase the greater the maximum numbers of animals in the population. More data are available for the small strain and these show that the relationship is not linear but the curve flattens out as r increases. Clearly there is a limit to the numbers of animals which can occupy a limited space and this is evidently approached as r reaches its maximum possible value. Data for the large strain are not sufficient to indicate how the curve flattens as r increases. In contrast to these two insects, the two values of maximum numbers for *R. dominica* show no trend with increase in the value of r. This may be because these values lie on the flattened part of what is a curvilinear relationship. The results as a whole suggest a relationship between r and the maximum numbers in the population but the relationship is different for the dif-

TABLE II. Showing the variability of populations shown in Figs. 1-4. The figures in the body of the table are the means of the four coefficients of variability (per cent) for the monthly counts within the period shown.

Weeks	*C. oryzae* Small strain Maize 29.1°C (Fig. 1)	*C. oryzae* Large strain Maize 29.1°C (Fig. 1)	*C. oryzae* Small strain Wheat 29.1°C (Fig. 2)	*C. oryzae* Large strain Wheat 29.1°C (Fig. 2)	*R. dominica* Wheat 29.1°C (Fig. 3)	*C. oryzae* Small strain Wheat 32.3°C (Fig. 4)	*R. dominica* Wheat 32.3°C (Fig. 4)
4-10.....	31	29	28	35	45	50	40
10-26.....	25	30	18	11	17	27	14
26-42.....	31	20	30	30	26	52	19
42-58.....	32	28	36	50	31	44	19
58-74.....	29	23	16	18	23		
74-90.....	28	16	14	13	21		
90-106.....	24	18	11	10	20		
106-122.....	..	..	..	..	19		
122-138.....	..	..	..	..	14		
138-154.....	..	..	..	..	14		
154-170.....	..	..	..	..	14		
170-186.....	..	..	..	..	10		
186-190.....	..	..	..	..	14		

ferent beetles. Figure 5B shows that when the densities of the populations at their maxima were expressed in units of weight instead of numbers, the general slope and shape of the curves were the same, but the relative positions of the curves for the two strains were reversed. At their maxima the small strain achieved greater numbers than the large strain but, since the individuals were relatively much lighter, the population of the small strain weighed less than the population of the large strain at its maxima.

When I began these experiments I expected to find that the maximum numbers of each beetle which could live in a given volume of grain would depend only on the amount of grain. The relationship which has been shown in Figure 5 between maximum numbers and r with one and the same species was quite unexpected. Another unexpected feature of these experiments was the observation that even at their greatest numbers the insects usually had consumed less than 30 per cent of the available food by the time it was due to be replenished. This amount was highly variable in the different experiments. As an example the data in Table IV show the amounts eaten by populations living at 29.1° C at the time when their numbers were about maximal.

The incomplete utilisation of food available to the populations suggests that (a) the food which is not eaten is not available for the insects or (b) factors other than food shortage limit the numbers. As to (a) it is possible that some of the food which is not consumed is not available to all stages of the insects. The hollowed out grains are not eaten by the larvae of *Calandra*. But the small pieces of grain left in cultures of *Rhizopertha* are eaten both by larvae and adults; this is simply demonstrated by breeding larvae through on these small pieces and by providing adults with these pieces and

TABLE III. The calculated logistic equations for the populations shown in Figs 1-4.

Species	Food	Temp. °C	Moisture content %	Logistic equation
C. oryzae (small strain) Fig. 1	Maize	29.1	13	$N=\frac{395}{1+e^{5.0598-0.2987t}}$
C. oryzae (large strain) Fig. 1	Maize	29.1	13	$N=\frac{220}{1+e^{5.0291-0.4588t}}$
C. oryzae (small strain) Fig. 2	Wheat	29.1	14	$N=\frac{950}{1+e^{6.3289-0.5514t}}$
C. oryzae (large strain) Fig. 2	Wheat	29.1	14	$N=\frac{500}{1+e^{5.7448-0.5221t}}$
R. dominica Fig. 3	Wheat	29.1	14	$N=\frac{466}{1+e^{5.4306-0.5022t}}$
R. dominica Fig. 4	Wheat	32.3	14	$N=\frac{550}{1+e^{4.9912-0.4788t}}$
C. oryzae (small strain) Fig. 4	Wheat	32.3	14	$N=\frac{540}{1+e^{7.0490-0.4183t}}$

TABLE IV. The amount of grain in grams which disappeared from 12 grams within two weeks when the density of adults approached maximum numbers for the experiments. Each figure is a mean of 25 estimates from cultures at 29.1° C and at 70% relative humidity.

Species	Grain	Number of adults		Weight of grain which disappeared	
		Mean	Range	Mean	Coefficient of variability
C. oryzae (small strain)	Wheat	715	602-816	3.57	29
C. oryzae (small strain)	Maize	398	174-558	2.25	35
C. oryzae (large strain)	Wheat	503	430-563	3.69	13
C. oryzae (large strain)	Maize	322	260-400	3.10	25
R. dominica	Wheat	382	287-501	1.53	25

nothing else on which to feed. Besides husks and small pieces of grain, there was always quite a large proportion of whole grains left in the cultures at the end of two weeks. Some of these grains were removed from cultures and provided as the sole food of larvae and adults. In each case the grain was utilised by these insects. When grain is not replenished at all, it is eventually reduced to dust before the last insect dies. The total evidence thus suggests that more food is available during the two-week intervals than can be eaten by the number of insects present. More insects could be crowded into the space available and presumably these

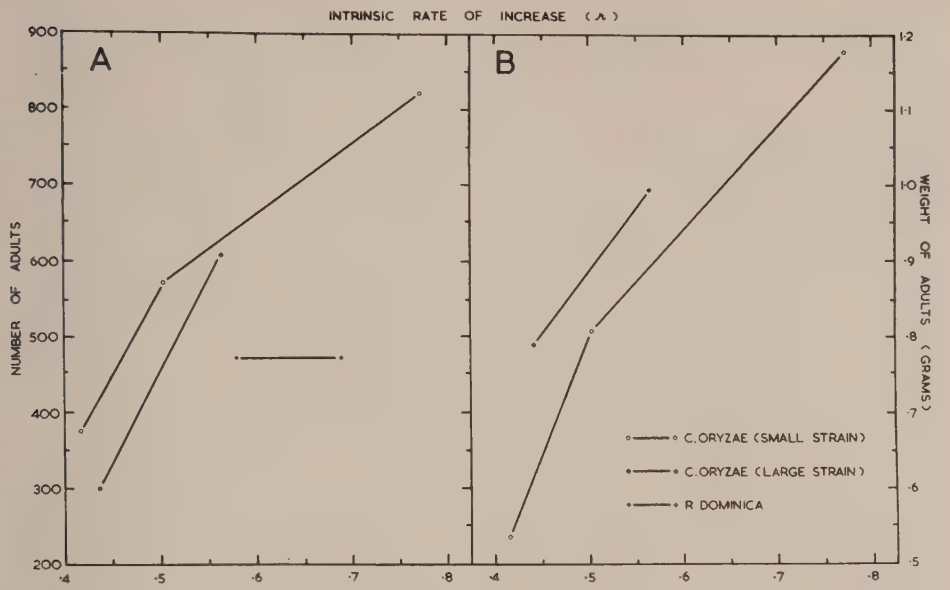

FIG. 5. The relationship between the innate capacity for increase r and (A) the maximum numbers of adults in experimental populations and (B) the maximum weight of adults in experimental populations.

would eat more of the grain. But the numbers are always something less than the limit imposed by space alone. Evidently neither space nor food shortage are the ultimate limiting factors to the numbers.

It is known that crowding of *Calandra* and *Rhizopertha* reduces fecundity (Birch 1945a); larval crowding increases mortality of the immature stages of *Rhizopertha* (Crombie 1944), the same is probably true of *Calandra*. The rate of larval development of *Calandra* is also reduced by crowding (Birch 1945b). Crowding is known to decrease the length of adult life of other insects, for example *Drosophila* (Pearl, Miner and Parker 1927); this probably happens in beetles also. Influences of crowding, such as these, evidently restrict numbers to something less than that imposed by space and food alone.

Now it has already been shown that numbers bear a relation to the innate capacity for increase of the populations. A hypothetical model can be constructed to show that this would be expected if crowding influenced the rate of increase in a certain way. Let us imagine a species to have an innate capacity for increase r_x at temperature x and a higher innate capacity for increase r_y at temperature y. Let us suppose that these populations grow in limited spaces at these temperatures. The actual rate of increase, as distinct from the innate capacity for increase, will fall off as density increases, until it is zero when maximum numbers are reached. For the purposes of this argument it does not make any difference if numbers then oscillate or simply follow an asymptote. We are interested in what happens at the maximum densities which will be referred to as K_x and K_y. Up to the maximum density, birth rate (b) exceeds death rate (d) but, at the maximum density, birth rate equals death rate; this is because birth rate decreases with increased density and death rate increases. Let us assume that the relation between density and birth rate and between density and death rate is linear. The hypothetical model can then be represented by Figures 6A and 6B. In Figure 6A the

line b_x represents the birth rate at different densities of the species at temperature x; d_x represents the death rate at temperature x. As the density of the population increases the birth rate exceeds the death rate until a density is reached where b_x equals d_x. This is the density K_x where the two lines intersect.

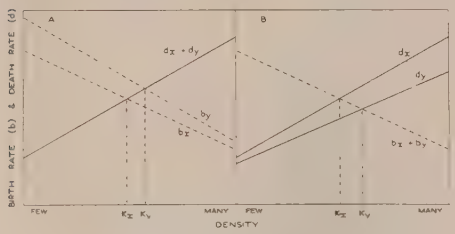

FIG. 6. Hypothetical model showing the effect of increased innate capacity for increase through (A) increased birth rate and (B) decreased death rate, on the maximum numbers in the population when the proportional effect of density on these components remains unaltered.

This is the maximum density, since at higher densities death rate exceeds birth rate.

Now in Figure 6A we have supposed that at temperature y the species has a higher innate capacity for increase by virtue of a greater birth rate b_y whilst the death rate d_y is the same as d_x. The line b_y runs above b_x but is not parallel to it as it has been assumed that the proportional change with density is the same for the two populations. The lines are separated by a constant proportion and not a constant amount. We now see that b_y and d_y intersect at a higher density, *i.e.*, K_y exceeds K_x.

Since the innate capacity for increase r = birth rate − death rate, the higher innate capacity for increase at temperature y could be due to a lower death rate. This situation is represented in Figure 6B. Again the effect is to increase the maximum density of the population. The corollary to be drawn from these examples is that a population with a higher innate capacity for increase (*i.e.*, a higher birth rate or a lower death rate) has a higher upper limit to its numbers.

If the relationship between density and birth rate and/or death rate at temperature x were very different from that at temperature y then there would not necessarily be any relation between the innate capacity for increase and the upper limit to numbers. It is, of course, still possible that there could be a relationship, but it would not be the relationship suggested in the examples just discussed. We are not in any position to suppose that these hypothetical models correspond with the experimental models described in this paper. They merely indicate one possible way of interpreting the interesting results of the experimental models.

Regrettably little data are available which would enable a comparison of the upper limit to numbers and the innate capacity for increase of other species. The data of Holdaway (1937) on *T. confusum* are suggestive. He grew populations in flour at three different relative humidities; 25 percent, 50 percent and 75 per cent. The upper limits to numbers in these populations were 8, 11 and 15 adults per gram respectively. He did not determine the innate capacity for increase at these different humidities but enough is known about the biology of the beetles to be assured that r must be smallest at 25 percent relative humidity and largest at 75 per cent relative humidity. Holdaway himself stated that he considered the lower maxima at lower humidities were due to lower net fecundity and slower speed of development at lower humidities.

Innate Capacity for Increase and the Logistic Curve

We have seen that the logistic curve provides an empirical description of part of the trends of the experimental populations shown in Figures 1-4. Bearing in mind the particular limitations of the logistic curve in relation to these data, we may nevertheless use the data to examine one of the basic assumptions of the logistic theory. It is the way in which the theory makes use of the concept of r. The theory assumes that the population commences growth with an initial rate

of increase r which is the intrinsic rate of natural increase; it is the constant rate of increase it would have if it were increasing in an unlimited space so that density might be considered to be continuously at an optimum. But as each individual is added to the population when it is growing in a limited space the rate of increase is considered to be reduced by a constant amount. This involves the assumption that every individual makes an equal demand on the resources available to the population. The propositions of the logistic theory may be expressed in symbols. The equation for the geometric increase in unlimited space is:

$$\frac{dN}{dt} = rN \quad . \quad . \quad . \quad . \quad . \quad (1)$$

and the rate of increase of the same population growing in a limited space becomes:

$$\frac{dN}{dt} = (r - cN\ )N \quad . \quad . \quad (2)$$

In this expression N is the density of the population and c is the constant amount with which, we postulated, the rate of increase was reduced by the addition of one individual to the numbers already in unit space. The rate of increase thus continues to be reduced as a linear function of N as N becomes larger until at some maximal value of N, cN approached r and $r - cN$ approached O.

Equation (2) is the differential form of the logistic curve. It is more instructive to include in the equation the symbol K which stands for the maximal or asymptotic value which N approached as t (time) approached infinity. As N approached this asymptote the rate of increase approaches O. So we can write when $N = K$:

$$\frac{dN}{dt} = \text{O}; \quad \text{and } r - cN = \text{O}$$

hence $r - cK = \text{O}$

$$\text{and } c = \frac{r}{K} \quad . \quad . \quad . \quad . \quad . \quad (3)$$

Substituting in equation (2) we get:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad . \quad . \quad . \quad (4)$$

In the integral form this equation may be written:

$$N = \frac{K}{1 + e^{\,a - r\,t}} \quad . \quad . \quad . \quad (5)$$

This is the form of the curve which is usually employed in fitting the logistic curve to experimental data. The logistic theory thus provides us with an independent method of estimating the innate capacity for increase r for those populations to which the theory is applicable. Table V and Figure 7 allow a comparison between the estimate of r derived from the life table and the age fecundity schedule (Birch 1953) and that derived from the logistic equations fitted to the data shown in Figures 1-4. For each example the estimate of r from the logistic curve is somewhat smaller than that from the life table and age schedule of fecundity. Even so the agreement of the two estimates is remarkably close, especially when it is remembered that the value of r of the logistic equation is derived from the growth of the adult population only.

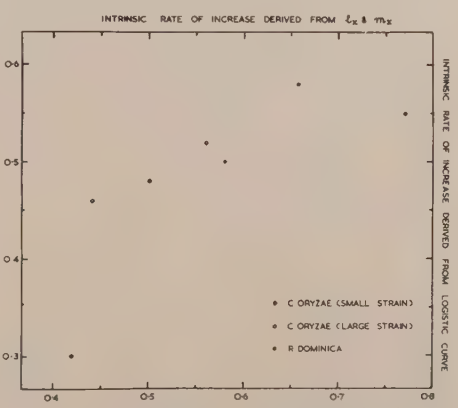

FIG. 7. The correlation between the innate capacity for increase r derived from the life table and age schedule of fecundity and that derived from the logistic curve.

The agreement is closest in those populations in which the growth trends fitted the logistic equation for a large part of the initial sigmoid trend.

These results would tend to support the concept that there is an attribute of

TABLE V. Two independent estimates of the innate capacity for increase (expressed as the intrinsic rate of natural increase) for the experimental populations.

Species	Grain	Temp. °C	Moisture content of grain, %	The innate capacity for increase (r)	
				Derived from the life-table and age-fecundity table	Derived from the logistic curve
C. oryzae (small strain)....	Wheat	29.1	14	0.772	0.55
R. dominica.....	Wheat	32.3	14	0.686	0.58
R. dominica.....	Wheat	29.1	14	0.578	0.50
C. oryzae (large strain)....	Wheat	29.1	14	0.564	0.52
C. oryzae (small strain)....	Wheat	32.3	14	0.501	0.48
C. oryzae (large strain)....	Maize	29.1	13	0.436	0.46
C. oryzae (small strain)....	Maize	29.1	13	0.417	0.30

animals corresponding to the innate capacity for increase.

UNFULFILLED ASSUMPTIONS OF THE LOGISTIC THEORY

The logistic theory has a limited empirical application in describing the trend of populations shown in Figures 1-4. Nevertheless we have also seen that these data support the assumption of the logistic theory that there is an attribute of animals corresponding to the concept r, the innate capacity for increase. The limitations of the theory in failing to provide a completely adequate empirical description of the growth trends of these populations must be sought in the remaining assumptions of the theory which we have not yet examined in relation to these data. There are four of these:

(a) That the rate of increase ($\frac{dN}{dt}$) is an inverse linear function of density, *i.e.* that the rate of increase is decreased by a constant amount for each individual added to the members already present in unit space. There is no particular evidence either for or against this proposition provided by the data in this paper and so I shall not examine it any further here.

(b) That the population has a stable age distribution.

(c) That its density has been measured in appropriate units.

(d) That the influence of density on rate of increase operates immediately, *i.e.* that the rate of increase is slowed down to the full extent demanded by the theory immediately each additional animal is added to the population and not only at some later date. Or in other words, that there is no time lag associated with the influence of density on rate of increase.

(b) *The age distribution of experimental populations*

The theory of the logistic curve involves the assumption that the population commences growth with an intrinsic rate of increase r and this is only given when the initial population has a stable age distribution. A second feature implicit in the theory is that the initial age distribution remains unaltered during the growth of the population. Now neither these nor any other experiments on the growth of populations, of which I know, have been initiated with populations of stable age distributions. This is due, in part, to the difficulty of working with the large numbers that would be required, but it also seems that the need to fulfill this condition had been overlooked until Leslie (1948) pointed out the significance of the stable age distribution for the logistic theory. Theoretical considerations by Leslie (1948) showed that a population of stable age distribution would retain its stable age distribution when living in a limited space only if the birth rate was independent of density and the changes in rate of increase were due solely to the influence of density on survival rate. But it is well known that the birth rate of insects does vary with density. In any case

there is no experimental evidence that these or other experimental populations do assume a stable age distribution.

The existence of an upper asymptote is also dependent on the continuance of the stable age distribution. If the age distribution were not of the stable form at the density of the upper asymptote then density would not remain constant. Instead it has been shown by Leslie (1948) that it would first fluctuate on either side of the asymptotic density K.

In view of the fact that the experiments of this paper were initiated with a pair of adult insects, and since there is no reason to suppose that the age distribution ever reached the stable form, it is not surprising to find that the logistic curve does not give a completely adequate description of the observed trends. Populations initiated with a few adults would have a faster initial growth than populations initiated with a group of animals of stable age distribution. There would be a tendency for numbers to overshoot the theoretical upper asymptote. This overshooting would be followed by an undershooting and this would be expected to continue until a stable age distribution was established.

(c) *The choice of units for representing the population*

The unit of the population is the individual animal. Provided the size of the individual is independent of the density of the population, the constants a and r in the logistic equation would have the same value independently of whether the population had been measured in numbers, weight or volume; but K would depend on the unit of measurement. The beetles in the experiments in this paper become smaller in crowded populations. The different sizes of adults from crowded cultures are shown in Table VI. The high densities shown in the table are about the same as the maximum numbers reached in the experiments; measurements were made on insects from cultures which had been oscillating about these densities for several months.

The addition of a large animal in the early stages of population growth might be expected to influence the rate of increase rather differently from the addition of a small animal in the latter stages. Equivalent results might come from the addition of the same weight of animals rather than the same number. This would appear to be the case in populations of blowfly larvae in meat (Ullyett 1950). Not sufficient data on weights of the beetles were obtained for testing whether the logistic theory gave a better fit when weights were used instead of numbers.

(d) *The instantaneous response in the rate of increase to change in density*

Referring back to equation (2), it is obvious, since this equation does not have

TABLE VI. The effect of density of adult insects on the size of adults of the two strains of *C. oryzae* bred in wheat and in maize.

Species	Grain	Number of insects per 12 grms of grain	Length of pronotum + elytra in mm.[1]		Mean weight in mg.[2]
			Mean	Coefficient of variability	
C. oryzae (small strain)	Wheat	20	2.44	8.3	1.600
C. oryzae (small strain)	Wheat	1000	2.26	7.5	1.433
C. oryzae (small strain)	Maize	20	2.64	5.0	1.858
C. oryzae (small strain)	Maize	1000	2.43	8.6	1.435
C. oryzae (large strain)	Wheat	20	2.84	4.1	2.450
C. oryzae (large strain)	Wheat	500	2.51	8.8	1.643
C. oryzae (large strain)	Maize	20	3.19	4.0	3.280
C. oryzae (large strain)	Maize	500	2.89	8.0	2.637

[1]Based on 50 beetles. [2]Mean of 2 lots of 500 beetles.
Differences between mean lengths of each species at the high and the low densities are significant at P=0.01.

any modifying factor associated with cN, that the equation implies that the quantity in the bracket is always less than r by a quantity exactly equal to cN, *i.e.* that the quantity cN changes immediately N changes. If this were not to be implied, the equation would contain a modifying factor for time associated with cN. But then the equation would no longer describe a simple sigmoid curve like the logistic. In applying the logistic equation we would have to be satisfied that the rate of increase in experimental populations growing in limited space does in fact respond immediately to changes in density. But there is reason to suppose that this may not be so. There are two aspects to this problem; it is known that fecundity and mortality do not necessarily react immediately to changes in density; secondly certain aspects of animals with life histories involving a number of different stages such as the egg, larva, pupa and adult of an insect, make it unlikely that the rate of increase would react immediately to changes in density.

It is not necessary to review here all the evidence for a lag in the influence of density on the fecundity and mortality of insects. It is inconceivable that the addition of an extra individual to a population would decrease the survival rate of that population immediately. The effect of crowding on mortality takes time. I have already pointed out that crowded cultures produce smaller insects and these will have a different effect on the population from the same number of larger insects; there is a lag of at least one generation before crowding has this particular effect of reducing the size of the animals. The smaller adults probably lay fewer eggs. This has been demonstrated in *Drosophila* (Chiang and Hodson 1950; Robertson and Sang 1944) and *Plodia interpunctella* (Snyman 1949).

The other quality of insects which makes it likely that there is a lag in the effect of crowding is the complex life history. Each stage of the life history makes a different contribution to density and at least with larvae and adults this will vary with age. The addition of N eggs to the population is not the same as the addition of the same number of larvae or adults. If N eggs are added to the population, in due course some of them become larvae and some of them become adults and the rate of increase of the population will be decreased as they grow and utilise more of the resources of the environment. The interval which elapses between the laying of the egg and the emergence of the adult is a measure of the time lag which occurs in the influence of density on rate of increase.

The overall effect of time lag in the effect of density must be for the population to grow faster than would be expected according to the logistic theory. This would result in a tendency for an overshooting of the theoretical asymptote with a corresponding tendency for a subsequent undershooting of the asymptote. This effect may be responsible in part for the oscillations which occurred in the experimental models (Figs. 1-4).

This section might be summarised by saying that in three respects the requirements of the logistic theory do not apply to the experimental models described in this paper. The importance of measuring numbers rather than weights cannot be assessed but it is possible that weight would have been a more adequate measurement. The discrepancies between theory and experiment are in the direction and of the order that might have been expected from populations which lacked the stable age distribution and in which the influence of density on rate of increase operated with a time lag. These two influences could act together to produce the oscillations in numbers which are so characteristic of the experimental populations. These effects evidently have a sustained and long-term influence judging from the long-term nature of the oscillations. For example, the small strain of *C. oryzae* in wheat at 29.1° C had a complete oscillation in 45 weeks; this represents about 5.4 generations. The existence of oscillations in the numbers of animals growing in limited space with a

constant food supply is of great interest because it highlights some factors which cause animal numbers to change. Oscillations like those described here have been recorded in experimental populations of *Daphnia magna* (Pratt 1943), *Tribolium confusum* and *T. castaneum* (Park 1948) *Trogoderma versicolor* (Park, Gregg and Lutherman 1941), *Callosobruchus chinensis* (Utida 1941) and *Lucilia cuprina* (Nicholson 1950). Indeed it would seem that oscillations are characteristic of laboratory populations of animals with complex life histories which have been studied for a sufficient length of time to enable the experimenter to detect them. This may be a general characteristic of animals with complex life histories as compared with organisms with simple life histories such as *Paramoecium* and yeasts. These latter populations tend to conform more closely to the logistic curve (see Gause 1934).

The experimental models described in this paper are considerably more complex than the theoretical model of the logistic theory of population growth. This does not imply that the logistic theory is of little value in interpreting the trends in these experiments. It would seem that the theoretical model needs to be a good deal more flexible than the logistic theory allows. This provision may be more suitably dealt with by means of a "stochastic" treatment which is drawing the attention of some population mathematicians (*e.g.* Kendall 1949) rather than by the "deterministic" approach of the logistic theory.

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Summary

The maximum number of insects which occurred in the oscillations of five out of seven series of experimental populations grown in a limited space with a constant food supply was correlated with the innate capacity for increase (r) of the populations. The particular relationship was different for the three beetles. The experimental models were compared with a hypothetical model in which such a relation between r and the upper limit to numbers would be expected provided the proportional effect of density on the reduction of the rate of growth of the population was independent of the innate capacity for increase. The upper limit to numbers in the experimental populations was not simply due to food shortage or insufficient space to hold any more insects, but to the particular way in which crowding affects the rate of increase.

All seven experimental populations showed an initial sigmoid trend which was followed by long term oscillations. Each oscillation took about a year to complete. The trend in numbers only partly conformed to the logistic curves calculated to fit the data. Departure from the logistic trends was associated with a number of conditions of the logistic theory which were not fulfilled in the experimental models: the age distribution was not of the stable form; the insects were smaller when density was great, so that it is questionable whether numbers really represent the best measure of the growth of the populations; and there was a lag in the effect of density on the rate of increase. On the other hand the constant r (the innate capacity for increase) in the logistic equation corresponded remarkably well with an independent estimate of this index derived from the life table and the age schedule of fecundity. This provides corroborative evidence that r is a real characteristic of animals and that it has a reality in the logistic theory which can be substantiated.

The time lag in the effects of density on the rate of increase and the non-stable age distribution could both have ac-

counted for the oscillations in numbers obtained in the experimental models. Such oscillations are probably to be regarded as a general characteristic of experimental populations of insects and other organisms which have many stages in the life cycle.

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A COMPARISON OF SURFACE SOIL PROPERTIES UNDER MESQUITE AND PERENNIAL GRASS

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Since the settlement of the Southwest, velvet mesquite (*Prosopis juliflora* var. *velutina* (Woot.) Sarg.) has invaded large areas of former semidesert grassland range. Formerly confined mainly to the alluvial soils of the primary drainages, this tree-like shrub has become established on many new sites which encompass a considerable range of soils, topography, and climatic conditions. The resulting loss in grazing capacity and difficulty in handling livestock have centered attention on the processes involved in the invasion and methods which are economically feasible for control of mesquite.

Studies by Glendening (1952) and Brown (1950) have shown that once invading trees reach seed-producing size, mesquite may be expected to become the dominant species of the vegetative cover. After it has passed the seedling stage, velvet mesquite successfully competes with the herbaceous undercover for the limited moisture which occurs throughout the semidesert type.

Invasion is accompanied on areas of continual heavy grazing by a reduction in density and vigor of the grasses and accelerated soil movement. The widespreading lateral root system and the open crown canopy of mesquite are not effective in stabilizing the soil or contributing to its improvement. As the stand of mesquite continues to thicken, the effects of soil erosion become more prevalent; roots of the perennial grass are often exposed and the soil surface becomes noticeably more irregular.

The results of a comprehensive analysis of soil samples obtained from an area of rangeland which is currently undergoing the transition from perennial grass to mesquite are presented in this paper. They are intended to supplement other ecological findings on the spread of mesquite and to provide an indication of accompanying edaphic changes on one widespread soil type.

The soil samples were obtained from the Santa Rita Experimental Range in southeastern Arizona. The herbaceous plant cover of the sampled area consisted principally of black grama (*Bouteloua eriopoda* (Torr.) Torr.), and Rothrock grama (*B. rothrockii* Vasey), interspersed with small islands of approximately 40-year-old velvet mesquite (Fig. 1). The annual precipitation for the site averages approximately 16 inches, of which 45 per cent occurs during the winter as low intensity, general storms, in contrast to most of the remainder which falls as violent summer thundershowers.

The soil of the area has been typed by Young, *et al.* (1931) as Tumacacori coarse, sandy loam. It is an important and extensive component of the soils of the upper mesa and foothills of the experimental range. The surface soil is a dark brown, coarse, sandy loam which varies in thickness from several inches to about one foot. It grades into a medium brown, coarse-textured loam at three to four feet. The subsoil is generally loose and open and irregularly stratified with many gravelly layers.

In general, soils of the Tumacacori series are without developed horizons, compaction, structural development, or accumulation of clay and colloidal materials. They have developed from an alluvial-fan deposit of coarse, angular sand and fine gravel—mostly granite and syenite. The coarse sandy loam phase of the Tumacacori series is favorable for grass growth; it absorbs and holds moisture

[1] Maintained by the Forest Service, U. S. Department of Agriculture, for Arizona, New Mexico, and West Texas, with headquarters at Tucson.

FIG. 1. Typical plant cover during the dormant period on the area where samples were obtained for analyses of the physical and chemical properties of the surface soil. U. S. Forest Service Photograph (H-67).

well, releases it readily to the plants, and is sufficiently rich in humus and nitrogen to support a vigorous plant growth.

EXPERIMENTAL PROCEDURE[2]

Soil samples were obtained from three carefully selected locations, all within 400 feet of each other. It was a requisite of each location that it contain the best grass cover available, paired with an adjacent stand of mesquite. Three soil samples were combined into a composite sample at each subsite under the grass cover and similarly three from the nearby mesquite-infested area. Those from within the mesquite stand were obtained outside the crown perimeter of the trees.

For the analyses associated with the volume of the soil in place, a duplicate set of samples of known volume was taken with a small shovel, especially constructed to contain 24 cubic inches. All samples were taken from the surface inch of soil during February 1951 when the upper six inches of soil were at field capacity.

Chemical and physical analyses of the soil samples were conducted according to standard laboratory techniques. Samples of known volume were tested for pore volume, volume-weight, and specific gravity using a pyrex desiccator and evacuation in cold water for 3 hours, essentially as described by Lutz (1944). Moisture equivalent was determined by centrifuging a portion of each sample at 1,000 times gravity for 30 minutes as recommended by Veihmeyer, *et al.* (1930). Moisture equivalent was used to estimate field capacity, which when expressed by volume was subtracted from the total pore volume to determine air capacity. The texture of the samples was determined by the Bouyoucos hydrometer technique

[2] The author is indebted to Dr. H. J. Lutz of Yale University, School of Forestry, for his guidance in the laboratory analysis of the soil samples.

(Bouyoucos 1936) for the silt and clay fractions; and by mechanical screening for subdivision of the sand separates. Separation of the heavy mineral portions of the samples was made according to the procedure given by Tamm (1922) using bromoform with a specific gravity of 2.68. Organic matter was determined by the chromic acid wet-combustion method (Peech, *et al.* 1947). Since the samples contained a high percentage of sand, loss-on-ignition tests were also made. The hydrogen-ion concentration of the samples was measured by the glass electrode method.

Other analyses included total nitrogen, exclusive of nitrate nitrogen, by the modified Kjeldahl method and readily available phosphorus using Truog's stannous chloride method with a photoelectric colorimeter (Truog 1930). Exchangeable calcium and potassium were determined by the macro-methods described by Peech, *et al.* (1947). The cation exchange capacity of the samples was determined by distillation of absorbed ammonia following extraction with sodium chloride of the ammonium saturated soil which remained after the exchangeable cations had been leached out (Peech, *et al.* 1947). Exchangeable hydrogen was determined with a pH meter according to the procedure proposed by Brown (1943). Per cent base saturation was obtained by subtracting the exchangeable hydrogen from the total cation exchange capacity and dividing by the total cations.

Results

The data from the physical and chemical analyses of the soil samples obtained under the two types of vegetation are shown in Tables I and II. The results of the laboratory tests cannot be fully evaluated by statistical treatment because the number of samples was, of necessity, limited. Nevertheless, statistically significant differences were found between the two groups of samples, with respect to some important textural and chemical characteristics. In other cases, the differences, while not significant at the 5 per cent level, were at least consistent between the paired counterparts.

The surface soil under the grass stand is significantly finer in texture than the surface soil under mesquite. Differences in moisture equivalent, pore volume, air capacity, and other physical properties also indicate that the mesquite soil has a

TABLE I. *Physical properties of surface soil samples obtained under perennial grass cover and interspersed stands of approximately 40-year-old mesquite*

Sample	Physical properties												
	Texture—American classification												
	% Fine gravel	% Coarse sand	% Medium sand	% Fine sand	% Very fine sand	% Silt	% Colloid	% Moisture equivalent	% Pore volume	% Air capacity	Volume weight (gms/cc)	Heavy mineral separation (%)	Specific gravity
Mesquite site													
1	9.7	22.5	23.0	16.9	6.2	16.1	5.5	6.71	42.0	32.0	1.53	13.8	2.64
2	12.8	22.5	20.2	15.1	6.2	17.8	5.7	7.06	43.7	33.2	1.48	9.5	2.63
3	14.0	23.6	20.8	15.0	6.1	15.1	5.3	5.47	37.0	27.9	1.66	16.9	2.64
Average	12.2	22.9	21.3	15.6	6.2	16.3	5.5	6.41	40.9	31.1	1.56	13.4	2.64
Grass site													
1	7.7	18.5	24.4	21.7	7.5	14.7	5.5	—*	46.6	41.8	1.46	15.4	2.73
2	9.8	21.0	21.7	17.7	7.0	17.5	5.3	7.25	45.1	34.8	1.43	8.6	2.60
3	9.1	18.7	21.3	17.7	6.9	20.7	5.5	7.05	45.6	35.3	1.46	11.8	2.69
Average	8.9	19.4	22.5	19.0	7.1	17.6	5.5	7.15	45.8	35.0	1.45	11.9	2.67
Level of significance of difference between means	.05	—	—	.05	.05	—	—	—	—	—	—	—	—

*Sample lost.

TABLE II. *Chemical properties of surface soil samples obtained under perennial grass cover and adjacent stands of approximately 40-year-old mesquite*

Sample	pH	Loss-on-ignition (%)	Organic matter (%)	Total nitrogen (%)	Available phosphorus (ppm)	Exch. calcium (%)	Exch. potassium (%)	Cation exchange capacity (me)	Exch. hydrogen (me)	Base saturation (%)
Mesquite site										
1	5.3	1.75	0.99	0.054	50	0.039	0.013	4.89	1.65	66.3
2	5.3	1.57	.85	.052	65	.039	.012	4.51	1.50	66.7
3	5.8	1.72	1.04	.050	48	.044	.012	4.17	1.20	71.2
Average	5.4	1.68	.96	.052	54	.041	.012	4.52	1.44	68.1
Grass site										
1	6.1	2.14	1.19	.066	39	.048	.016	4.85	1.65	66.0
2	6.0	1.78	1.02	.058	88	.047	.016	4.82	1.10	77.2
3	5.9	2.06	1.13	.061	55	.051	.016	5.04	1.55	69.2
Average	6.0	1.99	1.11	.062	61	.049	.016	4.90	1.43	70.8
Level of significance of difference between means	—	.05	.05	.05	—	.01	.02	—	—	—

less favorable structure and moisture regime than that under grass.

The analysis of the heavy mineral separate under the two conditions indicates that more soil movement has occurred under the mesquite. In this test the percentage of minerals which exceed 2.68 specific gravity averaged slightly higher where the grass cover has been replaced. This would appear to indicate that some of the lighter minerals had been carried away.

Chemical analyses show greater loss-on-ignition, and higher organic matter and exchangeable calcium content of the soil under grass compared with that under mesquite. All of these elements contribute to the maintenance of a desirable structure. The grass soil also has a higher nutrient capital as indicated by the total nitrogen, available phosphorus, and exchangeable potassium and calcium determinations. The differences are small, however, and probably not sufficient in themselves to preclude the re-establishment of grass on the mesquite soil following mesquite control.

DISCUSSION AND CONCLUSIONS

Differences in the physical and chemical soil properties which favor the presence of semidesert grasses are apparent in the comparison of the two groups of samples. That the observed differences are due to soil deterioration since invasion rather than to invasion of only the inherently poorer soils is indicated by early records and photographs showing that the coarse sandy loam soil of the Tumacacori series originally supported a uniform grass cover.

A more favorable moisture regime of the surface soil exists under the herbaceous type of vegetation. While the coarser texture of the mesquite soils permits higher infiltration, moisture is more rapidly lost through evaporation. Organic matter content of the soil is increased by the relatively short-lived, fibrous grass roots whereas the thick woody roots of mesquite contribute little even in the deeper soil layers. Repeated search for nodules of symbiotic nitrogen-fixing bacteria has failed to disclose any in the area of study.

Structure in the coarse granitic desert soils often consists of only a loose arrangement of smaller soil particles around a central larger grain (Fletcher and Beutner 1941). This is easily dispersed, however, and the finer sand particles are removed since they possess little cohesive-

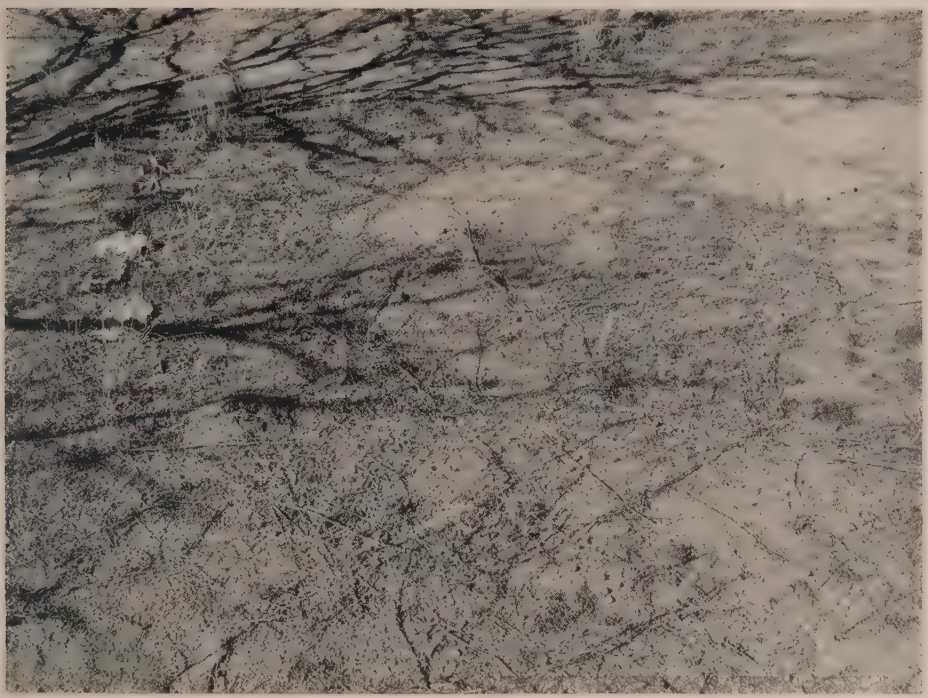

FIG. 2. Coarse sandy soil with little herbaceous ground cover under trees of a stand of 40-year-old mesquite. Compare with foreground, Figure 1. U. S. Forest Service Photograph (H-72).

ness and insufficient mass to withstand the impact and carrying capacity of the water.

As shown in these tests, replacement of the grasses by mesquite has reduced the water-holding capacity and general fertility of the soil. While the individual differences are small, they are important collectively if the relationship among the various tests is recognized, inasmuch as each property contributes to the over-all quality of the site (Fig. 2).

The condition which now exists on the mesquite sides is one that is distinctly more favorable for the reproduction of mesquite than of the perennial grasses. Carefully controlled planting studies of velvet mesquite seeds have shown a higher percentage of germination and successful initial establishment on coarse-textured soils. In addition, the subsequent growth of seedlings is greater on the lighter soils. Other experimental plantings of mesquite seeds show that establishment of mesquite seedlings may be prevented or markedly reduced by the presence of a dense grass cover.

SUMMARY

Samples from the surface inch of soil from native black grama-Rothrock grama grassland areas and interspersed areas recently invaded by mesquite were analyzed for physical and chemical properties. The samples were obtained from the foothill vegetation type on the Santa Rita Experimental Range in southeastern Arizona. The soil of the sampling area is typed as a Tumacacori coarse sandy loam.

The laboratory analyses indicate the soil under the mesquite cover to be deteriorated in both chemical and physical properties. The latter is believed of greater importance since the indicated reduction in the nutrient capital is not believed to have reached the minimal requirements of the grasses.

Physically, the soil under the mesquite was coarser, lower in pore volume, and

higher in volume-weight. Soil structure and moisture relations were apparently less favorable and there was shown to be more instability of the surface soil.

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SOME NORTH AMERICAN TURTLES AND THEIR EPIZOOPHYTIC[1] ALGAE

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That certain algae occasionally grow on the carapaces of turtles is a fact well-known to many persons, scientists and laymen alike; hardly a person has not heard of "mossback" turtles, and the term "mossback" has been incorporated into our language. In view of the wide familiarity with the phenomenon it is remarkable that there apparently never has been a systematic study of this interesting relationship, either on the part of the phycologists or the herpetologists. In the preparation of the present study many herpetological papers that mention epizoöphytic algae (or "moss") have been examined; only three of these (Evermann and Clark 1916; Lagler 1943; Walker, Green and Jones 1953) even give generic determinations of the algae. Neither of the two recent major works on North American turtles (Pope 1939; Carr 1952) gives this relationship more than passing remarks. Of eleven herpetological works which note the presence of algae on turtles, four involve the musk turtle, *Sternotherus odoratus* Latreille, seven the snapping turtle, *Chelydra serpentina* Linnaeus; one the painted turtle, *Chrysemys picta* Schneider; and one Blanding's turtle, *Emys blandingii* Holbrook (Carr 1940; Conant 1938; Lagler 1943; Pope 1939; Cahn 1937; Ruthven, Thompson and Thompson 1912; Brimley 1942-1943; Schmidt 1938; Loennberg 1894; Minton 1944; Walker, Green and Jones 1953). In addition to these species certain others are noted in the literature. Cahn (1937) reports algae growing on the alligator snapper, *Macrochelys temmickii* Troost (see also Carr 1952, Fig. 7, p. 56), and Loennberg (1894) discusses "parasitic algae" on the striped mud turtle, *Kinosternon baurii* Garman.

The phycologists have been somewhat better about determining the turtles upon which they have found algae. Collins (1907) reports *Basicladia chelonum* (Collins) Hoffman and Tilden on *Chrysemys picta marginata* Agassiz and *Sternotherus odoratus;* Tiffany (1926) reports *B. chelonum* from *Chrysemys p. bellii* Gray; Tiffany (1937) records *B. chelonum* from *Chrysemys p. marginata* and *Basicladia crassa* Hoffman and Tilden from *Chelydra serpentina;* and Hoffman and Tilden (1930) originally described *B. crassa* from *Chelydra.* These and other observations have shown that the currently known species of the fresh-water algal genus *Basicladia* apparently are restricted to the shells of turtles, having never been reported growing on other substrates. In addition to *Basicladia, Dermatophyton radicans* Peter (1886) was originally described from turtles.

The nature of the turtle-alga relationship presents a difficult problem. Allee *et al.* (1949, p. 243) cite it as an example of commensalism, which they define as a symbiotic relationship in which one partner is benefited and the host not particularly harmed. Such a definition reconciles well with the fact that algae of the genus *Basicladia* are entirely restricted to the epizoöphytic "habitat." What

[1] In view of the confusion regarding the use of the term *epizoic,* Tiffany (in Smith, *et al.,* 1952) used the term *epizoöphytic* to cover symbiotic relationships involving plants living upon animals. The editor (E. S. D., a student of zoophytes) regards this coinage as unfortunate; by ecologists' usage, if not by logic (see Naumann's "Limnologische Terminologie," Vol. II of Abberhalden's "Handbuch der biologische Arbeitsmethoden"), *epiphytic* and *epizoic* refer to organisms that grow on plants or animals, respectively.

these algae gain from their turtle hosts is difficult to determine, although *Basicladia* must gain something from the relationship. The benefit to the algae may be the result of an extremely subtle positive selection; possibly the simple motility which epizoöphytism confers is an advantage over non-motile types. That some such advantage is present seems patent from the host-epizoöphyte specificity described here. This benefit would certainly be tenuous, but it may have had great evolutionary significance. Camouflage for the turtle, which has recently been suggested by Harper (1950) and which seems so obvious to humans, would seem of little importance in view of the general absence of organisms predatory upon adult turtles.

Materials and Methods

Algae were obtained from turtles available in the collection of one of us (R. A. E.) and we are indebted to Dr. Orlando Park for allowing us access to specimens in the collection of Northwestern University. Over 700 turtles were examined; of these 549 were *Chrysemys picta* ssp.

As would be expected, most of the algae encountered were of the genus *Basicladia*. Generic determination provided no particular difficulty; however, the two species of *Basicladia* are separated chiefly on the basis of size. Filaments of *B. chelonum* seldom have a diameter of more than 50 μ, whereas those of *B. crassa* usually have a diameter of more than 50 μ, although some cells may measure as low as 40 μ. The smaller species never (or very rarely) has any branching other than basal; the larger species branches freely, both basally and laterally. With a small amount of material available, samples of *Basicladia* whose filaments measure near 50 μ are almost impossible to identify when branching is not evident. It is quite likely that the two species overlap in dimensions, and that confusion will occur unless great care is taken in identification. This might perhaps account for a portion of the ecological overlap noted below.

Most of the turtles came from midwestern areas, although a few were collected in other scattered areas in North America.

Results

Species Differences in Proportion of Epizoöphytism. Certain species of turtles seem to be heavily epizoöphytized, whereas certain others support little or no algae. These data have been summarized in Table I. Such differential proportions can hardly be explained on the basis of random distribution of algae on the various turtle species. In some species sufficient material has been examined to give reliable estimates as to the proportion of epizoöphytism. The highest proportion was found on *Sternotherus odoratus;* over half of the specimens examined showed the presence of algae. At the other extreme less than 10% of the specimens of *Chrysemys picta* bore algal colonies. *Graptemys* shows an even lower proportion of epizoöphytism; however, most specimens have not been identified to species. Of the two epizoöphytized *Graptemys,* one was a common map turtle, *G. geographica* Le Sueur, and the other a sawback turtle, *G. pseudogeographica* Gray. Fair numbers of *Clemmys* have been examined (17 spotted turtles, *C. guttata* Schneider, and 15 wood turtles, *C. insculpta* Le Conte), but no algae have been found on them. About 11% of the specimens of the slider turtle, *Pseudemys scripta* Schoepff, had algal growths. It is interesting to note that Cagle (1950) does not mention algae in his extensive ecological study of this species. Eight soft-shelled turtles, *Amyda ferox* Schneider, and one *Macrochelys* were examined; none was epizoöphytized.

The high proportion of epizoöphytism in *Sternotherus* may well be correlated with its highly aquatic habits, whereas the "sunning" habits of the "pond" turtles (*Chrysemys, Pseudemys, Graptemys*) may tend to reduce algal colonies by frequent desiccation. Algae may be excluded from the highly aquatic *Amyda* by the nature of the shell which is leath-

ery and quite different from the shells of the other species studied.

TABLE I. Differential proportions of turtles bearing epizoöphytic algae.

Species of turtle	Number turtles examined	Number turtles with algae	% with algae
Pseudemys scripta	35	4	11.4
Chrysemys picta	549	52	9.5
Amyda ferox	8	0	0
Emys blandingii	15	6	40.0
Sternotherus odoratus	66	36	54.6
Chelydra serpentina	20	8	40.0
Graptemys sp.	44	2	4.5
Clemmys guttata	17	0	0
Clemmys insculpta	15	0	0
Kinosternon sp.	5	2	40.0
Macrochelys temminckii	1	0	0
Undetermined	5	0	0
Total	780	110	14.1

On the basis of the data presented three classes of turtles may be erected on the basis of proportion of epizoöphytism: 1) those which apparently do not support algal growths (*Amyda, Clemmys guttata,* and *Clemmys insculpta*); 2) those which support algae in low proportion (*Pseudemys, Chrysemys,* and *Graptemys*); and 3) those which are frequently epizoöphytized (*Sternotherus, Chelydra, Emys,* and *Kinosternon*).

Species Specificity in the Algal-Turtle Relationship. Table II shows the distribution of the various species of algae encountered on the various species of turtles. The two species of *Basicladia* are the most common epizoöphytes. *Basicladia chelonum* has been found on specimens of *Kinosternon* and *Graptemys pseudogeographica; B. crassa* has been found on *Emys;* and both species have been found on *Chrysemys, G. geographica, Chelydra, Sternotherus,* and *Pesudemys.* If one assumes that colonization of the carapace by the algae is the result of their random distribution one would expect about an equal distribution per species of turtle. Such results have not been obtained in the present study. Of 35 *Chrysemys* from which the algae were sampled and identified, 23 had only *crassa* colonies, 9 had only *chelonum,* and only 3 had both species; thus *crassa* was found on 74% of all of all epizoöphytized *Chrysemys* examined while *chelonum* was found on only 34%. On *Chelydra, B. crassa* was again the most important of the two algae (87%). *Sternotherus,* on the other hand, shows a higher proportion of *B. chelonum* (78%).

Assuming that the differential proportions obtained from the sampled turtles provide an accurate estimate of the "attack rates" of the algae on the turtles in nature, these rates present some interesting comparisons (Table III). These estimates suggest that *Chrysemys, Sternotherus,* and *Pseudemys* are "attacked" by *B. crassa* at relatively similar rates, whereas *Chelydra* has a much higher proportion of "attack" by this species. *Chrysemys, Chelydra,* and *Pseudemys* are only lightly epizoöphytized by *B. chelonum,*

TABLE II. Proportional distribution of various species of algae on the various species of turtles.

Turtle species	Number with Algae Identified	Algal Species											
		B. chelonum		*B. crassa*		*R. hieroglyphicum*		*D. radicans*		*C. glomerata*		*E rivularis*	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
C. picta	35	12	34	26	74								
E. blandingii	5	..	..	4	80	..	..	..	..	1	20		
G. geographica	1	1	100	1	100								
C. serpentina	8	1	13	7	87	..	..	..	..	..	..	1	13
S. odoratus	27	21	78	6	22	1	4	1	4	..	..	2	7
Kinosternon sp.	2	2	100										
G. pseudogeographica	1	1	100										
P. scripta	4	3	75	2	50								

whereas a large number of *Sternotherus* is colonized by this species.

TABLE III. Estimated "attack rates" of epizoöphytes on various turtle species.

Species	Attack Rate (% of total)	
	B. chelonum	*B. crassa*
C. picta	3	7
S. odoratus	43	12
P. scripta	9	6
C. serpentina	5	35

A possible explanation of this species specificity is provided by the habits of the turtles and the habitus of the algae. As was noted above *B. crassa* is a robust alga with a relatively large filament diameter, whereas *B. chelonum* has a small diameter. From these size relationships, implying a lesser surface: volume ratio in *crassa,* one would conclude *a priori* that this species is capable of withstanding a greater amount of desiccation than the smaller *chelonum.* The fact that *crassa* colonies develop more readily on *Chelydra* would seem explained by the fact that these turtles spend considerable amounts of time basking in the sun on logs, rocks, and banks. *Sternotherus,* on the other hand, is almost completely aquatic, seldom venturing from the water (Carr 1952); it is also highly nocturnal (Edgren 1944; Carr 1952), so that most of its limited land movement would be expected during the cool, damp night when algal desiccation would be least important. From these facts the smaller species would seem to be at a strong selective disadvantage when on the "sunning" species of turtles; thus *chelonum* is restricted to the more aquatic forms. *B. crassa,* by virtue of its larger size, should withstand better the conditions imposed by the basking of the turtles. The differing "attack rates" seem explained by the fact that *Sternotherus* is the most aquatic of these forms; *Chelydra* is also relatively aquatic, but spends considerable time basking; and *Chrysemys* and *Pseudemys* are sufficiently terrestrial in habits to keep all algae in low proportion.

In addition to *Basicladia* three other species of epizoöphytic algae have been discovered in the present investigation. *Cladophora glomerata* (L.) Kütz and *Rhizoclonium hieroglyphicum* (Ag.) Kütz have been found on an *Emys* and a *Sternotherus* respectively. The rare chaetophoralean *Dermatophyton radicans* Peter was also found on a *Sternotherus.* This is apparently the second report of *Dermatophyton radicans,* which was originally described from a turtle; other members of the genus may be epizoöphytic, epiphytic or free-living. An epiphytic blue-green alga (Myxophyta) *Entophysalis rivularis* (Kütz) Drouet was found on both *B. chelonum* and *B. crassa;* these *Basicladia* in turn were epizoöphytic upon *Sternotherus* and *Chelydra* respectively.

Unquestionably the two species of *Basicladia* are the most important of the epizoöphytic algae of North American fresh-water turtles. Interestingly enough, three of the four genera of epizoöphytes found in this study belong to the Cladophorales.

Distribution of Algal Colonies on Turtles. The position of algal colonies on various portions of the turtles presents some interesting data (see Table IV). Generally algae are found on the carapace. In most species they are so restricted; however, there are certain deviations. *Chelydra serpentina* commonly (6 specimens in 8) have algae growing on the dorsal spines of the tail, and one specimen had a colony on its head. The frequent (10 in 28) presence of green, photosynthetic algae on the plastron of *Sternotherus* is remarkable and suggests that *Basicladia* is able to live under conditions of very low light intensities. In addition to the plastron five specimens had colonies on the bridge which is also shaded to a great extent by the overhanging carapace. The single epizoöphytized specimen of *Graptemys geographica* also had growth on the plastron.

Colonies on *Chelydra* and *Sternotherus* are usually general in distribution on the carapace, whereas those on *Chrysemys* are most often around the edge (margi-

TABLE IV. Position of algal colonies on turtles (numbers indicate number of turtles with algae growing in the indicated positions).

Species	Position									
	Carapace						Plastron		Bridge	Other
	Anterior	Posterior	General	Vertebrals	Costals	Marginals	Anterior	Posterior		
G. geographica	..	..	1	..	..	..	..	1		
G. pseudogeographica	..	..	..	..	1	1				
Kinosternon sp.	..	1	1							
P. scripta	2	..	1	..	..	1				
E. blandingii	..	1	1	..	2	3				
C. serpentina	..	1	7	..	..	..	..	..	..	6(Tail) 1(Head)
S. odoratus	1	1	14	3	5	7	4	7	5	
C. picta	1	4	6	3	27	39				

nals and costals) and seldom on the center (vertebrals). The frequent absence of algal colonies on the center of the *Chrysemys* carapace would seem explicable on the basis of the habits of the painted turtles. Although this species basks in the sun for considerable periods, it is also commonly seen floating at the surface, head and central portion of the carapace above the water. This would seem to indicate that algae on the center of the carapace would be subject to more frequent desiccation than algae on other parts. This may tend to exclude algae from the central portion of the carapace, while leaving the edges habitable.

Size of Epizoöphytized Turtles. Superficial examination seemed to indicate that only larger specimens of the turtles were epizoöphytized. According to Carr (1952) the subspecies of *Chrysemys picta* vary somewhat in size, and there is a sexual dimorphism in size. The smallest subspecies is *C. p. dorsalis* Agassiz, and the smallest hatchling was 22 mm. in length (Carr 1952, pp. 214-234). The smallest epizoöphytized *Chrysemus* examined was 64 mm. in length. Thus *Chrysemys* seems to be colonized only when several times hatchling size. Furthermore, the smallest sexually mature female examined by Cagle (1942) had a shell 95 mm. in length; only 4 of the 47 epizoöphytized *Chrysemys* that were measured had a carapace less than that value. From these data it seems obvious that algal colonies grow only on the larger painted turtles.

The same relationships hold for *Sternotherus;* the smallest hatchling noted by Carr (1952 p. 84) measured 21.0 mm., whereas the smallest turtle bearing algal colonies was 79 mm. in carapace length.

In Table V similar mensural data are included for the other species of epizoöphytized turtles. In all cases the smallest colonized individual was considerably larger than hatchling size. There seems no clear explanation for this phenomenon; perhaps younger turtles shed the carapace laminae at a more rapid rate than older individuals.

TABLE V. Size comparisons of smallest epizoöphytized individual with hatchling size in various turtles.

Species	No. of specimens epizoophytized	Smallest epizoophytized	Smallest hatchling*
G. pseudogeographica	1	105 mm	32 mm
K. subrubrum	1	92	24
P. scripta	4	145	29
E. blandingii	4	174	33
C. serpentina	7	175	29
C. picta	47	64	22
S. odoratus	14	79	21

*Data from Carr, 1952.

Other Ecological Factors. The explanations suggested for the relationships described above are those which appear most probable to us; other factors, not

discussed, however, may have considerable effects. Geographic area, type of water body, season, etc., may all have served to modify the relationships, but, when one is working from museum specimens, critical data of this type are frequently not available. The samples of turtles studied were primarily (over 70%) from lakes in southeastern Wisconsin, northeastern Illinois, northern Indiana, and southwestern Michigan, the "Chicago Area" and surrounding regions (Edgren and Stille 1948); therefore, broad geographic variations probably have had little effect. In addition these lakes are of relatively similar age and appear to have relatively similar vegetations which would tend to provide similar environments. Although more extensive material from differing habitats may show varying effects upon the relationships, our data from relatively homogeneous areas show no obvious differences.

The apparent specificities (*B. chelonum* on *Sternotherus* and *B. crassa* on *Chelydra*) probably have not been the result of seasonal differences. All musk and snapping turtles were collected during the late spring to early fall (May through September). *Sternotherus* specimens with *B. crassa* colonies were taken in May, July, and September. The single *Chelydra* with *B. chelonum* was collected in August. Turtle size also had no apparent effect upon these specificities. Of the group of *Sternotherus* which were measured, two, the smallest and the next to the largest, had *B. crassa,* and all intermediates had *B. chelonum.* The single *Chelydra* with a *B. chelonum* colony was about average size.

Evolution of Alga-Turtle Relationships

Both the green algae among the plants and the turtles among the animals represent ancient groups of organisms (Arnold 1947; Carr 1952). The singular association of these two ancient groups, as represented in recent times by *Basicladia* and the turtles, may be indicative of a long history of the relationship, and perhaps a mutual evolution between epizoöphytic algae and habitat preference of the turtle hosts.

The early turtles are considered to have been marsh dwellers, the highly aquatic and highly terrestrial turtles being secondarily derived. It seems a relatively minor shift in ecological niche from the various inanimate substrata inhabited by most algae to the shell of an aquatic turtle. One may assume that this transfer occurred many times, by means of flagellated spores or other spore lodgment and still takes place today, as such normally non-epizoöphytic genera as *Rhizoclonium* and *Cladophora* have been found on turtles. The algae may have evolved reciprocally with the turtles, new algal forms developing as certain turtles became more terrestrial. These changes would have placed selective advantage upon desiccation tolerance, presumably through such modifications as a smaller surface: volume ratio, more water-impermeable cell walls, physiological adjustments to dryness, etc. On the other hand, algal evolution may have been subsequent to the adaptive radiation of the turtles; in such a case one would expect similar algal development in response to similar selection pressures, but in already opened ecological niches.

The present relationship between the algal genus *Basicladia* and the turtles is probably explicable on the basis of the second method suggested above, and is probably of relatively recent origin. As a result of its more frequent occurrence upon highly aquatic turtle species, *Basicladia chelonum* may be presumed to be the more primitive of the two species, and thus the more similar to the early *Basicladia* stock than is *B. crassa. Basicladia crassa* may be considered to have developed from *B. chelonum* or a primitive *chelonum*-like ancestor by invasion of niches provided by relatively more terrestrial turtles and subsequent physiological and morphological modification. The presence of an ecological overlap (*B. chelonum* on turtles normally inhabited by *B. crassa* and *vice versa*) would seem to

indicate that this development is not yet complete.

Summary

The well-known phenomenon of epizoöphytic algae living upon turtles has never been subjected to systematic study. The nature of the relationship has never been clearly defined, although it seems best considered as commensalism as defined by Allee *et al.* (1949).

Many turtles of certain species are epizoöphytized (*Sternotherus odoratus*), other species show few epizoöphytized individuals (*Chrysemys picta*), and some show none at all (*Clemmys insculpta* and *C. guttata*). The singularly epizoöphytic genus of algae, *Basicladia,* has two species, one of which (*B. chelonum*) most frequently inhabits the shell of the highly aquatic *Sternotherus;* the other species (*B. crassa*) is most commonly found on *Chelydra* which basks in the sun, but is still relatively aquatic. Neither alga apparently has colonized the frequently sunbasking pond turtles (*Chrysemys, Pseudemys*) with any major degree of success.

Algal colonies tend to be differently distributed over the shells of the various species of turtles. They are generally found on the carapace, although they have been found on the plastron, bridge, tail, and head. In *Chelydra* and *Sternotherus* the algae are found all over the carapace, but on *Chrysemys* growth is generally restricted to the edge of the shell. Smaller and presumably younger turtles of a given species are generally not epizoöphytized.

Our data show no obvious geographic, habitat, or seasonal effects on algal attack-rates, nor does turtle size appear to affect the algal specificities.

The algae may be presumed to have evolved reciprocally with their turtle hosts, or to have invaded the new niches provided by the adaptive radiation of the turtles. In recent times *Basicladia crassa* probably evolved from the more aquatic *chelonum* or from a *chelonum*-like ancestor.

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SOME SAMPLING CHARACTERISTICS OF A POPULATION OF RANDOMLY DISPERSED INDIVIDUALS[1]

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INTRODUCTION

As our knowledge of plant communities increases, greater emphasis is being placed on the methods used to measure the characteristics of these communities. Succeeding decades have shown a trend toward the use of quantitative methods, with purely descriptive studies becoming less common. One reason for the use of quantitative techniques is that the resulting data are not tinged by the subjective bias of the investigator. The results are presumed to represent the vegetation as it actually exists; any other investigator should be able to employ the same methods in the same communities and secure approximately the same data. If such is not the case, the so called quantitative methods are worse than valueless, since they lend an aura of false accuracy that may be very misleading. To make certain that his results are reproducible, the worker must be sure that his sample is adequate, that the location of his sample has been made without bias, and that the limitations of his method are understood.

The student of plant communities is concerned with the distribution of objects in space. His first problem is the determination of the kinds of plants present and their relative numbers. Since it is usually impossible to examine all of the plants present, he confines himself to some kind of a sample of the vegetation. This may be in the form of area samples, as quadrats or belt transects; line samples, as in the line intercept method; exclusion angle methods; or any of a variety of point samples. In each of these cases, the results are affected in their accuracy by the actual dispersion of the plants on the ground. The plants may be regularly distributed as on the corners of squares or hexagons or in other definite patterns, so that every individual is equally distant from each of its nearest neighbors; they may be grouped into distinct clumps, as in the aggregated or so-called contagious distributions (Short 1845, Goodall 1952); or they may be distributed in an intermediate or random fashion.

Many of the methods now in use presuppose a random distribution of individuals in the population and are satisfactorily accurate when such conditions prevail. However, since many herbaceous plants are not randomly distributed (Ashby 1948, Whitford 1949, Steiger 1930), it is essential that a knowledge of their actual distribution be determined before the usual measurements may be interpreted properly. To date, no completely suitable method for assessing the random or non-random nature of plant distributions has been proposed. Before such a method is developed, it will be necessary to understand in detail the characteristics of a random population. This paper is concerned with an analysis of some of the characteristics of such a random population.

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Artificial versus natural populations

The ideal way to study random plant distributions would be to find such a distribution in nature and apply field techniques to it but for obvious reasons this cannot be done. A more practicable approach is to construct a map of a population from a set of coordinates derived from a random numbers table which has already been subjected to exhaustive tests for randomness. Fortunately, such random numbers tables exist. The use of an artificial population map has other advantages in that it can be sampled over and over again without the inevitable destruction that accompanies field sampling; sampling points on the map can be located quickly and with great accuracy; and the parameters of the population are known.

Random distributions

The concept of a random distribution is not easy to define. In general, it can be said that each of the objects making up the population is located independently of all others, so that any object has an equal and independent chance of occurring at any locus. There is an absence of fixed pattern—the objects are not located at fixed distances from one another nor is there a marked gradient from regions where the population is dense to regions where it is rather sparse. Any major portion of the population will have approximately the same number of objects as any other equal portion, but within each portion there will be areas of greater than average density and there will be distinct bare areas. No two random populations will be exactly alike, but all will have the above mentioned characteristics.

Numerous tests have been used to determine whether or not a population is random. Perhaps the most well-known is comparison with a Poisson distribution, which is used with area samples (Blackman 1935). Briefly stated, if a number of area sampling units of equal size are laid down on the population, it is possible to determine from the Poisson distribution how many of them should include no individuals, how many should include one individual, two individuals, etc. A comparison of the actual results obtained from an area sample with the expected results from a Poisson distribution calculated from the sample mean, using a suitable test of significance, makes it possible to determine whether or not the results differ significantly from those that would be expected from a population with the individuals distributed at random. With artificial populations, the dispersion of the individuals is checked by dividing the map of the population into many equal areas by means of grid lines; each area is then considered to be a sample of the population equivalent to a quadrat of the same size. It should be pointed out that populations other than random populations can be constructed which will fit a Poisson distribution when sampled in this manner. An arrangement with the individuals distributed in a regular manner, but with the densities of different areas varying along a gradient from dense to sparse will fit a Poisson. Other populations could be constructed with the individuals grouped into various sizes of clumps that also might fit a Poisson distribution. In view of these facts, it is apparent that additional tests must be employed. One such test concerns geographical homogeneity. The population map may be divided into quarters, fifths, or into rows and columns, and the numbers of individuals present in each portion compared with the expected numbers by means of the chi-square test of homogeneity (Snedecor 1946). In this case it is assumed that each major area of the map will have an equal number of individuals, and the expected numbers are the total number of individuals divided by the number of equal areas into which the map has been divided. Greig-Smith (1952) has suggested grouping the individual grid units into blocks and using analysis of variance to determine variation between blocks as a method for determining geographical homogeneity.

An arrangement of the individuals showing absolute regularity, as exemplified by the trees in an orchard, will possess absolute geographical homogeneity, so this test also is insufficient by itself to determine randomness. Both of these tests are in a sense negative since failure of a population to conform to either of them definitely indicates that the population is not random, but the fact that a population does fit a Poisson distribution or does possess geographic homogeneity is no real assurance that the population is random. Use of both of these tests gives considerably more assurance than the use of either one of them alone, but the results can never be absolutely positive. However, the possibility of factors other than chance entering into the distribution of individuals is much less in an artificial population constructed from an adequately tested random numbers table than in a natural population in the field.

Methods

Construction of the population map

Several criteria were used in the planning of the population map employed in this paper. It was desired that the population contain a fairly large number of individuals and that the individuals be so designated that they could be grouped into species containing varying percentages of the total population. It was also desired that the ultimate grid units be at least as small as the finest unit used to measure distances. It was decided to have 1,000 individuals placed on a population map one square meter in area. The finest unit of the grid was one millimeter, so that there were one million points available for occupancy, only 0.1 per cent of which were actually used. The use of such a low percentage of the total possible points is an insurance against regularity. A coarse grid with most of the points occupied will have tendencies toward a regular distribution with the distance between individuals equal to the distance between points on the grid. The individuals were placed on the grid by means of a set of random coordinates supplied by the University of Wisconsin Computing Service. These coordinates were taken from a set of 400,000 random digits punched on IBM cards. Each IBM card had 40 columns of digits, and 6 of these columns were used. The columns to be used were chosen at random, and the deck of IBM cards was entered at a random point, so that the choice of numbers was entirely a matter of chance. The digits were tabulated directly onto a paper tape, and each set of 6 digits which made up a single pair of coordinates was numbered serially. The entire operation was performed by the machine so that there was no chance of personal bias in the choice or printing of the numbers.

The coordinates consisted of 6 numbers, such as 936 874. The first 3 represent the number of millimeters from the point of origin along the x axis, the last 3, the number of millimeters from the point of origin along the y axis. The base map was constructed on a piece of millimeter-ruled graph paper one meter square. Each decimeter line was heavily ruled and each centimeter line had a lighter ruling, but this ruling was heavier than the ultimate millimeter rulings. The decimeter lines represented the first digit of each coordinate and the centimeter lines the second digit. Through the use of these accented lines, and with the aid of an L-shaped ruler, ruled in centimeters, it was possible to locate each point on the map with fair speed. The intersections of millimeter lines on the graph paper were the exact locations of the points designated by the coordinates. Each individual was numbered serially as it was placed on the population, so that it was possible to establish species having any number of individuals from one to 1,000 by using blocks of the numbered individuals to represent a species.

After the base map had been completed, a tracing paper overlay was made, and this was reproduced by means of the

Ozalid process. The finished map contained none of the grid lines used to establish the locations of the individuals. It was deemed necessary to sample the population by means of a grid that was independent of the grid used to establish the locations of the individuals, since use of the same grid might result in a number of sampling points being placed directly on top of the individuals in the population.

The population was tested for randomness by means of the two tests previously described. For the geographical tests, the map was divided into quarters, fifths, 10 vertical columns, 10 horizontal rows, rectangular areas equal to 1/20 of the map area each, and square areas equal to 1/25 of the map area each. In all of these cases, the probability values were .50 or greater by the chi-square test for homogeneity, indicating that in a similar sample of another random population, the chances of getting a better fit were in all cases no better than even.

For the comparison with a Poisson distribution, 5 centimeter grid lines were used to divide the map into 400 equal areas, and the number of individuals was counted in each of these areas. The

TABLE I. *Comparison of the distribution of the individuals on the population with a Poisson distribution*

Number of individuals per quadrat	Observed number of quadrats	Expected number of quadrats
0	31	32.9
1	87	82.2
2	104	102.6
3	71	85.5
4	61	53.4
5	33	26.6
6	9	11.1
7 and over	4	5.7
	400	400
$\bar{X}=2.205$	$\chi^2=6.35$	$P=.40$

results are shown in Table I. The probability in this case is about .40, indicating that 60 times out of 100, a random population will give a better fit. It can be seen from the table that the deviations from the expected values follow no pattern. Regular distributions have too few samples with no individuals, too many samples with the mean number of individuals, and no samples with many individuals. Aggregated distributions, on the other hand, have too many samples with a large number of individuals and too many samples with no individuals. No marked trend toward either regularity or aggregation can be found in Table I. Rather, the deviations appear to be random fluctuations, with the greatest deviation being too few samples with 3 individuals, which is counterbalanced by too many samples with 4 and 5 individuals. Another Poisson distribution was run with the map divided into 100 equal areas. The probability was about the same, and again no trends were discernible.

The sampling of an artificial population presents one problem which is not usually serious when sampling in the field. This is the problem of the border. The individuals of the population have as much chance of being placed near the border as at any other location on the map. The points at which the sampling units fall can similarly be at any locus. Hence, it is possible for quadrats to be placed with parts of them extending over the edge of the map. The same difficulty arises when sampling with the exclusion angle methods used in this paper.

This problem can be avoided by discarding all sampling units, parts of which extend over the edge of the map, but this might result in an inadequate sample of the areas immediately adjacent to the edge. A more satisfactory alternative is to delimit an area immediately adjacent to the edge of the map as a border area. This area is considered to be an extension of the population within which no samples are laid down, but which is equal in density and species composition to the population in the interior. The actual population for which parameters are de-

termined and within which all the sampling points fall is thus reduced by the size of the border, but any samples which extend over the population into the border are counted just as though they were entirely within the population proper.

The width of the border was determined by balancing the desire to have the usable population as large as possible against the need to minimize border effects. It was decided that the border should be sufficiently wide that the distance from an individual in the interior of the population to its closest neighbor would be less than the distance from that individual to the outer edge of the border. A border equal in width to the square root of the mean area satisfies this requirement.

The parameters of the population with the border area excluded are as follows: area—8835.96 sq. cm.; number of individuals—882; mean area—10.018 sq. cm.; square root of mean area—31.65 mm. Mean area is defined as the average area occupied by a single individual and is obtained by dividing the area of the map by the number of individuals on it (Curtis and McIntosh 1950). The mean area of a species is the area of the map divided by the number of individuals of that particular species. The term, then, is an expression of the spacing of the individuals. In this paper, when the mean area of the entire population is being considered, mean area will be called population mean area.

When the individuals in the population are divided into 10 species by grouping serial numbers 1-100, 101-200, etc., relative densities vary from 9.41% to 10.54% as compared to the 10.00% value for each in the total population and mean areas of the species vary from 95.01 to 106.46 sq. cm. as compared to the 100.00 sq. cm. value for each in the total population. It can be seen that the exclusion of the border area has not greatly changed the parameters of the population.

Sampling methods

Since the individuals on the population were considered to be points without area, no measure involving cover could be used. Instead determinations of frequency and density were made. The methods used can be considered under two categories, the area methods and the exclusion angle methods involving distance measurements. No attempt was made to include a great variety of methods since the primary aim was not a study of methods, but rather a determination of the characteristics of the population as measured by various procedures. It was known on the basis of previous work with area samples (Cottam 1951) and with exclusion angle methods (Liebherr 1952) that related methods behave similarly on random populations.

The area samples were square quadrats of five different sizes. The sizes used were equal to ¼, ½, 1, 2, and 4 times the population mean area. Since the quadrat method is well-known to all ecologists, its mechanics will not be discussed.

The exclusion angle methods rely on the measurement of distance to arrive at density per unit area. Simplest of these is the use of a sampling point to choose an individual on the population—the individual closest to the point being taken—and the measurement of the distance from this individual to its nearest neighbor. This method will be called the closest individual method.

The other exclusion angle methods use other criteria for the determination of the individuals to which distances are measured. They are of two types, those in which the distance from the sampling point to various objectively chosen individuals is measured, and those in which the distance from the individual closest to the point to one or more objectively chosen individuals is measured. There are a wide variety of these methods—11 are discussed by Liebherr (1952)—and one of each type is used in the present

study. They are the point centered quadrant and the random pairs methods.

The quadrant method divides the area around the sampling point into four equal parts. On artificial population maps this is easily accomplished by the use of a piece of clear sheet plastic with two perpendicular lines engraved on it. The sheet is placed with the intersection of the two lines directly over the sampling point; distances are measured from this point to the closest individual in each of the four quadrants. At each point four distances and the species of the four individuals are obtained. In terms of numbers of individuals sampled, this method is comparable to a quadrat of a size equal to four times the population mean area. Variations of this method include using the closest individual rather than the point as the center, and dividing the circle into 3, 6, or any other number of equal parts (Dice 1952).

The random pairs method (Cottam and Curtis 1949) involves the use of an angle of exclusion to determine the individuals between which distances are measured. The individual closest to the point is located and an angle delimited with its vertex at the point and its bisector on this closest individual. Any other individual falling within this angle is excluded, and the distance is measured from the individual closest to the point to the individual nearest to it outside the angle of exclusion. This method has been used in the field with angles of exclusion of 160° and 180°. In this study, angles varying from 0° to 340° have been used.

The population was sampled through the use of a type of stratified random sample called restricted randomization. After the border had been delimited, the remainder of the population map was gridded into 100 equal squares. Two points were placed at random by means of a random numbers table in each of these squares, making a total of 200 such points. These points were further subdivided into four groups of 50. Measurements with each of the methods were taken at the same set of points. This was done to make the measurements taken for each of the methods more strictly comparable. The advantages of this procedure are discussed by Goodall (1952) in connection with measuring the changes that take place in the vegetation of an area over a period of years.

Results

Density

As used in this paper, *area density* refers to number of individuals per unit area, *i.e.* per quadrat, per acre, per 100 square meters, etc., while *relative density* is a percentage of the total number of individuals present. Area density may be determined directly from quadrat data; the mechanics of converting distance measurements obtained with the exclusion angle methods to area density will be discussed later. Relative density is obtained directly from the original data for all methods. The total number of individuals of a species is simply divided by the total number of individuals of all species, and the result multiplied by 100 to convert it to per cent.

The differences between the various methods in determining density may be illustrated through the use of an analogy. Let us assume that the plants in the population are presented by colored jelly beans, each color representing a different species. These colored beans are interspersed at random among a much larger number of white jelly beans, which represent unoccupied space. The quadrat method is then analogous to taking a scoop and counting the number of colored beans, by color, which are picked up in each scoopful. From the volume of the scoop, the number of colored beans per unit volume may be determined. The relative number of each color may also be determined by dividing the number of each color of beans by the total number of colored beans. The exclusion angle methods arrive at relative density, in the terms of the analogy, by taking a handful

of the beans and recording by color—2 colored beans for the random pairs method or 4 colored beans for the quadrant method. Density per unit volume in this analogy would be achieved by obtaining a measure of the amount of empty space, most simply by counting the number of white beans encountered between successive colored beans—a rather rough analogy to the measurement of the distance between individuals.

Relative density

Determinations of the accuracy and variability of relative density measurements in a random population were made using the quadrat (two sizes), quadrant, and random pairs (180° angle) methods.

TABLE II. *Comparison of variation with changes in the relative density of the species and in the number of sampling units employed. Figures in the body of the table are standard errors expressed as a per cent of the mean, of the values of ten replicate samples for each combination of actual relative density and number of units*

Actual relative density in population	Number of units	Random pairs	2M Quadrats	Quadrants	4M Quadrats
10	10	65.3	71.4	51.4	49.6
20	10	45.7	54.2	31.2	34.5
40	10	30.4	39.1	21.3	23.6
10	20	45.8	49.7	35.6	35.8
20	20	33.8	42.8	21.1	26.1
40	20	19.4	32.3	14.4	18.2
10	50	28.8	32.5	22.5	25.3
20	50	22.7	25.2	15.4	17.0
40	50	12.2	18.8	10.6	12.6
10	100	19.2	19.9	19.8	18.6
20	100	13.1	16.2	14.1	11.2
40	100	8.9	13.3	7.9	9.2

Data were taken with each method at each of the 200 sampling points described earlier. Results are shown in Table II. The two quadrat sizes chosen were those most directly comparable to the two angle methods used. The angle methods differ from the area sample methods in that the number of individuals in each subsample, rather than the size of the sampling area, is constant. The quadrant method always measures 4 individuals at each point, the random pairs method 2 individuals. A quadrat of a size equal to 2 times the population mean area includes an average of 2 individuals every time it is laid down, and is thus comparable to the random pairs method. A similar relationship exists between the quadrant and the 4 times population mean area quadrat. Table II was constructed by subdividing the population into 10 species and recording the number of individuals of each species obtained in the first 10 quadrats of a given size, and in each succeeding set of 10 quadrats. Data for the random pairs and quadrant methods were obtained in a similar manner. Data for the 20 and 40 per cent species were obtained by combining 2 or 4—10 per cent species, and data for the larger number of sampling units were obtained by combining successive groups of 10 sampling units. The figures in the body of the table are coefficients of variation of the means (per cent standard error) of 10 sets of the number of sampling units and actual relative density of species indicated.

The table shows that there is an increase in accuracy with an increase in size of sample and actual relative density of the species in question. This is true regardless of the method used. It appears that the chief factor determining accuracy is the total number of individuals of the species encountered. A high total number of individuals may be achieved by using many sampling units in the case of the angle methods, with the number of sampling units necessary increasing as the relative density of the species in question decreases. An additional possibility with the quadrats is an increase in the size of the quadrat.

Figure 1 shows the values in Table II plotted against N, the average number of individuals encountered in the sample. The solid line is $\sqrt{\frac{N}{N}}$. The data appear to follow the trend indicated by this curve, which assumes a straight-line relationship on log-log paper. This relationship is

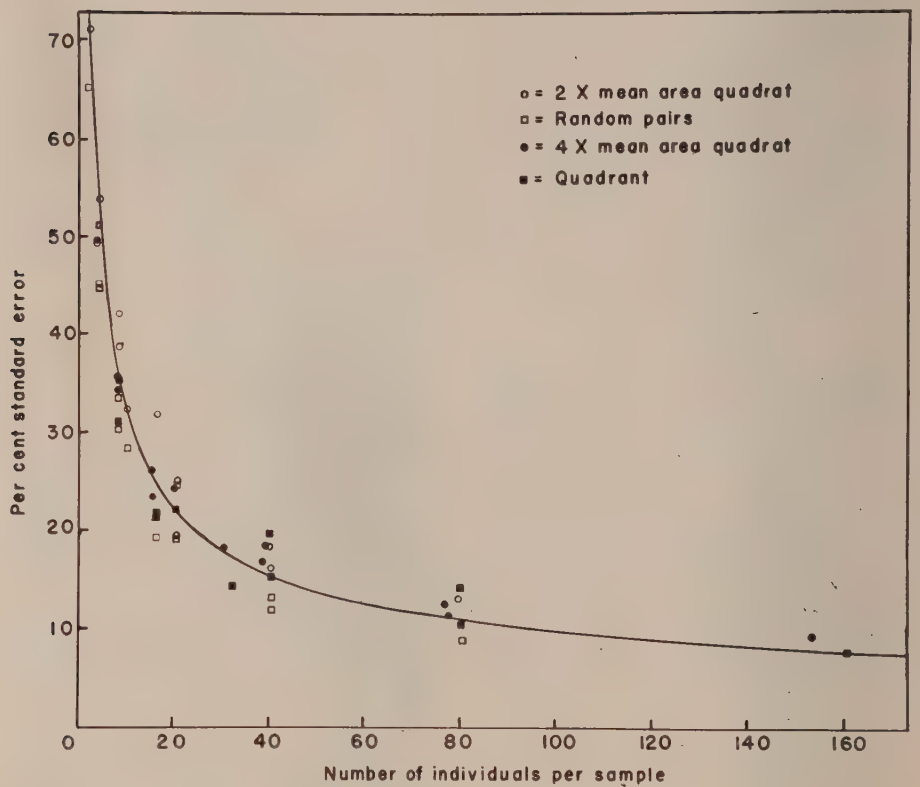

FIG. 1. The values in the body of Table II plotted against the average number of individuals encountered in each sample. The solid line is the square root of the number of individuals per sample divided by the number of individuals per sample.

commonly encountered in similar sampling problems (Hoppe and Holbert 1936).

When the individuals in a randomly dispersed population represent several species, the relative proportions of each species in the population may be determined with suitable accuracy by either area or angle methods. The main factor affecting such accuracy is the number of individuals that appear in the total sample. If a given species predominates in the population, the proportions may be determined accurately by a small sample. For species representing lesser and lesser fractions of the total, more or larger sampling units are needed to assess their correct proportions. As a general statement, it appears that about 30 individuals of a particular species should be encountered in the total sample before confidence may be placed in statements about its relative density.

Area density by quadrats

The determination of density per unit area by means of quadrat samples needs little discussion here. Results using five sizes of quadrats on the artificial population are shown in Table III. As was the case with the relative density figures, large quadrats give results more nearly approaching the correct values than do small quadrats, when the number of quadrats is held constant. The relative variability of subsamples of 50 quadrats is also less with the large quadrats than with the small ones.

TABLE III. *Mean number of individuals per quadrat for five quadrat sizes. Figures in the body of the table are means of successive subsamples of 50 quadrats*

Subsample number	Quadrat sizes in terms of population mean areas				
	.25	.50	1.00	2.00	4.00
1	.20	.54	1.04	2.30	3.92
2	.16	.34	.68	1.56	3.42
3	.18	.40	.84	2.06	4.12
4	.26	.36	1.00	2.14	3.92
Mean for 200 quadrats	.20	.41	.89	2.02	3.85

If the population is truly random, the number of individuals per quadrat should follow a Poisson distribution. Poisson distributions were calculated using mean number of individuals per quadrat of ¼, ½, 1, 2, 4, and 8. These distributions are shown in Figure 2. When the mean number of individuals per quadrat is low, the distribution is markedly skewed to the right, but as the mean gets larger, the distribution becomes broader, flatter, and more symmetrical. When curves for the actual distributions obtained from the quadrat data for the artificial population were compared with the theoretical Poisson distributions by the chi-square test of goodness of fit, the results did not differ significantly from those expected from a random distribution. Perhaps the most important feature of these area-density characteristics of a random population is the very great variation to be expected in number of individuals per quadrat when large quadrats (4 × mean area or larger) are used. When the mean density is 8 individuals per quadrat, 2 per cent of the samples will have 2 individuals or less, and 2 per cent will have 15 or more, but only about 40 per cent will have from 7 to 9 individuals.

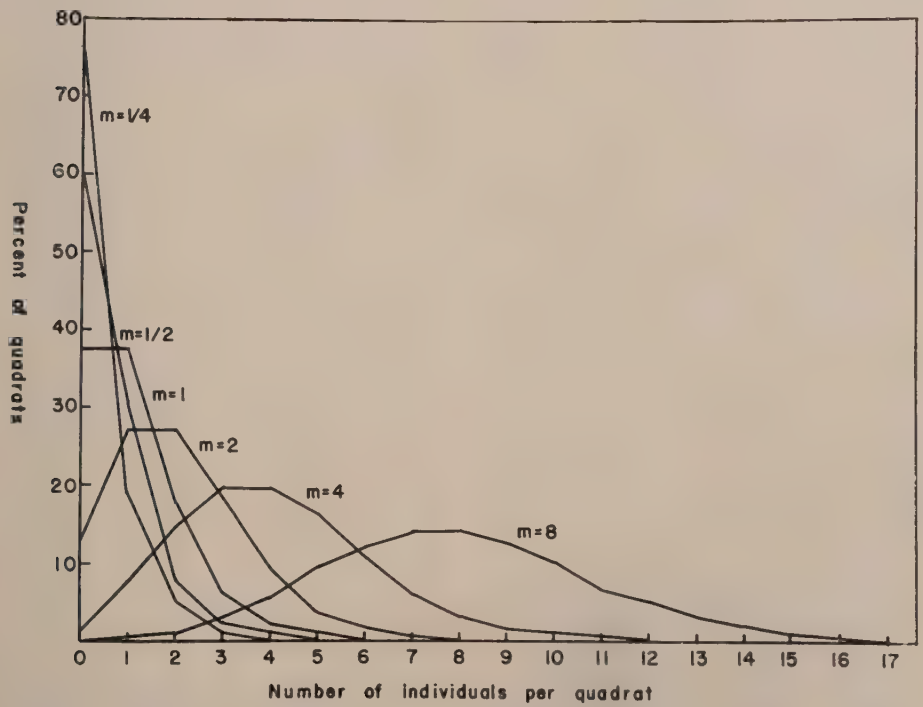

FIG. 2. Frequency polygons of Poisson distributions with different mean numbers of individuals per quadrat.

Area density by angle methods

With the angle methods, distance measurements are used to provide an estimate of density per unit area. The theory behind their use is that distances will vary with the density of the population, becoming smaller as density per unit area increases, and that the distances obtained by any objective method will bear a fixed relationship to the density of a random population. The conversion of these distance measurements to density per unit area is based on the assumption that the spacing of the individuals fluctuates at random from the condition in which they are an equal distance apart. The individuals may be considered to be located in the centers of squares, in which case the distance between individuals will be equal to the square root of the mean area. This is the *distance moyenne* of Braun-Blanquet (1932). The individuals may also be considered to be located in the centers of regular hexagons. Huesing (1932) has found tendencies toward such a distribution in some shrub communities. It has the theoretical advantage that each individual then occupies an area which is more nearly isodiametric. The distances in the case of a hexagonal distribution will be equal to 1.075 times the square root of the mean area (Cottam and Curtis 1949).

The distances derived through the use of either of these assumptions about the theoretical distribution of plants can be seen to bear a fixed mathematical relationship to one another. It is, therefore, not necessary, for the purpose of the paper, to consider which of these two hypotheses is the more valid. It is only necessary to have a standard by which the various distances may be compared. The simplest standard is the square root of the mean area, and this will be used throughout the paper.

Closest individual measurements

Because of the simplicity of this method, it was possible to take 100% samples rather than the samples from 200 points on which the data from the other methods are based. The distance was measured from each of the 882 individuals in the interior of the population to its closest neighbor. When this was done, it was found that many of the values were duplicates, individual A being closest to individual B, and individual B having individual A as its closest neighbor. The other alternative is for individual A to have individual B as its closest neighbor, but for individual B to be closest to some other individual. When these "paired individuals" were encountered, the distance between them was necessarily recorded twice, so that the data included 882 distances.

The most interesting results arising from the use of this method involve the consistency with which the measurements reflect the density per unit area of the population. By considering separate blocks of 100, 200, and 500 individuals to represent complete populations, it was possible to check the values obtained against population mean areas varying from 10 sq. cm. to 100 sq. cm. The results are shown in Table IV. It can be seen from the table that, in spite of a great variation in number of individuals per unit area, and a corresponding variation in the square root of the mean area of these populations, the results in terms of

TABLE IV. *Average distance between an individual and its closest neighbor for a series of populations differing in density per unit area*

No. of individuals in population	Square root of mean area	Av. dist. between individuals	Column 3 as per cent of column 2
34	137.1 mm	66.2 mm	48.28
41	125.1	67.0	53.55
54	108.9	54.3	49.86
68	103.1	53.0	51.40
75	92.3	46.8	50.70
152	69.6	34.6	49.71
403	45.4	22.3	49.11
425	44.2	20.8	47.05
882	31.6	15.3	48.41

per cent of the square root of the mean area are remarkably constant.

A comparison of the shape of the frequency polygons of the distances may be seen in Figure 3. Here the distances have been reduced to a common denominator by using varying class intervals to give an approximately equal number of distance classes for each population. The greater irregularity of the less dense populations is largely due to the fact that the size of the sample of these populations is smaller than is the case with the populations of higher density. Aside from this irregularity, the shape of the frequency polygons is very similar for each population density. They all possess a pronounced positive skewness. This type of distribution is often normalized by a square root transformation, and in this case square root transformations give values which, when tested by the g_1 statistic (Snedecor 1946) show no significant skewness.

Distances between closest individuals in a random population, then, bear a constant relation to the square root of the mean area. They are arranged about their mean in a Gaussian distribution when suitably transformed and hence may be subjected to further statistical treatment. Perhaps the most important attribute of these distances is their high coefficient of variation—averaging 54%.

Quadrants

The quadrant distance measurements were segregated according to the distance from the sampling point. For each sample, the quadrant in which the shortest distance was measured was designated Q_1, the quadrant in which the next shortest distance was measured was designated Q_2, etc. This provided four separate sets of data, the Q_1 data representing the distance between the individual closest to the sampling point and the point itself. The other quadrant figures do not necessarily measure the distance between the second, third and fourth closest individuals and the point, since any two, or even all four, of the closest individuals may be found in the same quadrant. In all cases, only the measurement between the point and the individual closest to the point in each quadrant was taken. Orientation of the sample was fixed, with the perpendicular lines separating the quadrants parallel to the grid lines on the population.

Table V gives a summary of these data. That the values for the means must increase from Q_1 to Q_4 is inherent in the method of collecting the data. In general, the standard deviation increases as the means of the distance increase. To quote Snedecor (1946), "It seems rather characteristic that large things vary much and small things vary little." To remove the inherent variability due to differences in the length of the distances, the coefficients of variation are shown in the last column of the table. The coefficient of variation is much greater for the Q_1 data than for the other quadrants. This is probably due to the fact that the distances obtained in Q_1 are more greatly influenced by the location of the sampling point than are the distances obtained for the other quadrants. The sampling point can theoretically land on an individual, which means that zero distances for Q_1 are possible. Values for the other quadrants can never be this small. The only possibility for small values for Q_2 is to have the sampling point land between two individuals that are close together.

TABLE V. *Summary of quadrant data. The last row in the table presents the results when the 4 distances obtained at each point are averaged*

Quadrant	Mean	Mean as % of sq. root of mean area	Standard deviation	Standard error	Coefficient of variation
Q_1.....	16.19 mm.	51.16%	8.02 mm.	0.57 mm.	49.54%
Q_2.....	26.02	82.22	8.40	0.59	32.27
Q_3.....	35.92	113.51	10.34	0.73	28.79
Q_4.....	50.10	158.32	15.16	1.07	30.25
Combined quadrants	32.05	101.30	7.60	0.53	23.71

This is an exceedingly rare occurrence. Usually, two individuals that are close together will be in the same quadrant, and distance will be measured to only one of them. The principal factor governing distance measurements for Q_2, Q_3, and Q_4 is the dispersion of the individuals on the population, and these values should vary as the density of the individuals varies from place to place on the population. Q_1 is also influenced by the density of the individuals on the population, but superimposed on this is the chance variation of the location of the sampling points with respect to the location of the individuals.

Values for the individual quadrants are of interest from the theoretical standpoint, but of more practical importance are the combined values. When the four quadrant distances from each sampling point are averaged, and these average values plotted, it is found that the frequency distribution is approximately symmetrical, with a g_1 value of 0.0311. The last line in Table V shows that these combined values are not only within 2 per cent of the value for the square root of the population mean area, but in addition possess a comparatively small standard error and coefficient of variation.

Random pairs

In many ways the random pairs method is similar to the quadrant method, and it would be expected that the results would show strong resemblances. The random pairs results are summarized in Table VI. That the mean should increase with increasing angles is inherent in the method. The mechanics of exclusion which bring this about are different from those used with the quadrants, but the end result is similar. Standard deviations increase with an increase in the mean, as before. The coefficients of

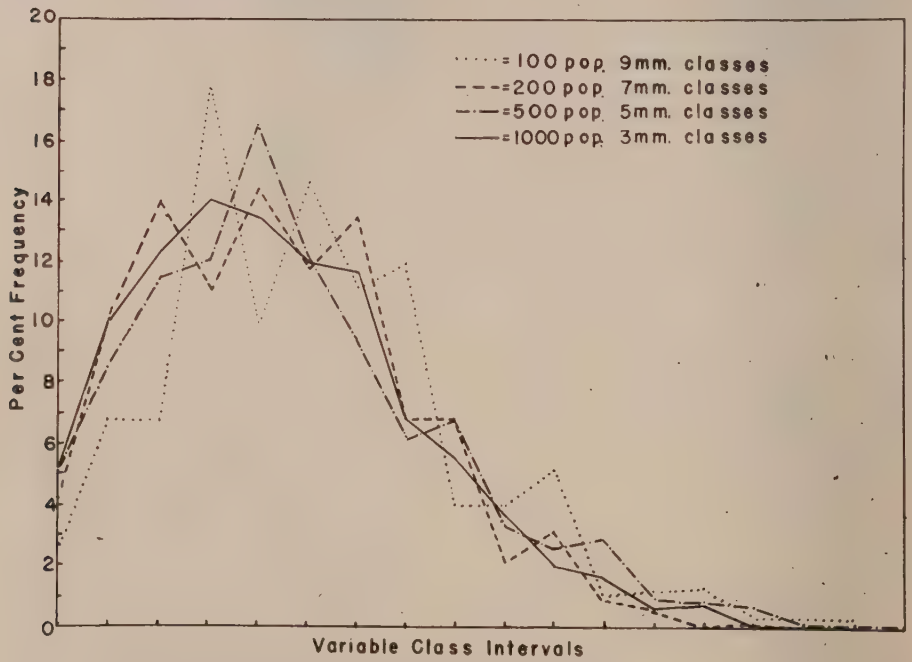

FIG. 3. Frequency polygons of the distances obtained through the use of the closest individual method. Variable class intervals have been used to show the similarities in the shape of the polygons.

TABLE VI

Angle	Mean	Mean as % sq. root of mean area	Standard deviation	Standard error	C.V.
0....	18.23	57.61	8.55	.60	46.90
30....	21.55	68.10	8.47	.60	39.30
60....	25.85	81.69	9.82	.69	37.99
100....	31.42	99.29	10.79	.76	34.34
140....	36.75	116.13	12.59	.89	34.25
180....	40.18	126.97	13.21	.93	32.87
220....	44.73	141.35	14.88	1.05	33.22
260....	49.11	155.19	16.16	1.14	32.91
300....	58.10	183.60	20.16	1.42	34.69
340....	80.65	254.81	33.39	2.38	41.40

variation also show similar trends, and for about the same reasons.

Column 3 of the table is plotted in Figure 4. The increase in the mean with increasing angles of exclusion is approximately linear until the two largest angles are reached, when the mean increases rapidly. Had larger angles of exclusion been used, the rate of increase would have been even more rapid. The curve will theoretically become asymptotic with the 360° ordinate, since angles of exclusion approaching 360 degrees will leave only an infinitely small area of the population in which individuals to which the distance is measured can be located, and these individuals will be, on the average, very far from the individual closest to the point.

Frequency distributions for the four quadrants and four selected angles of exclusion are shown in Figure 5. The most obvious changes that take place as the excluded area is increased are that the entire frequency distribution moves to the right and the distribution becomes broad and flat. There is an indication that the shape of the quadrant curves change. Q_1 is skewed to the right, not because of a long right hand tail but because of

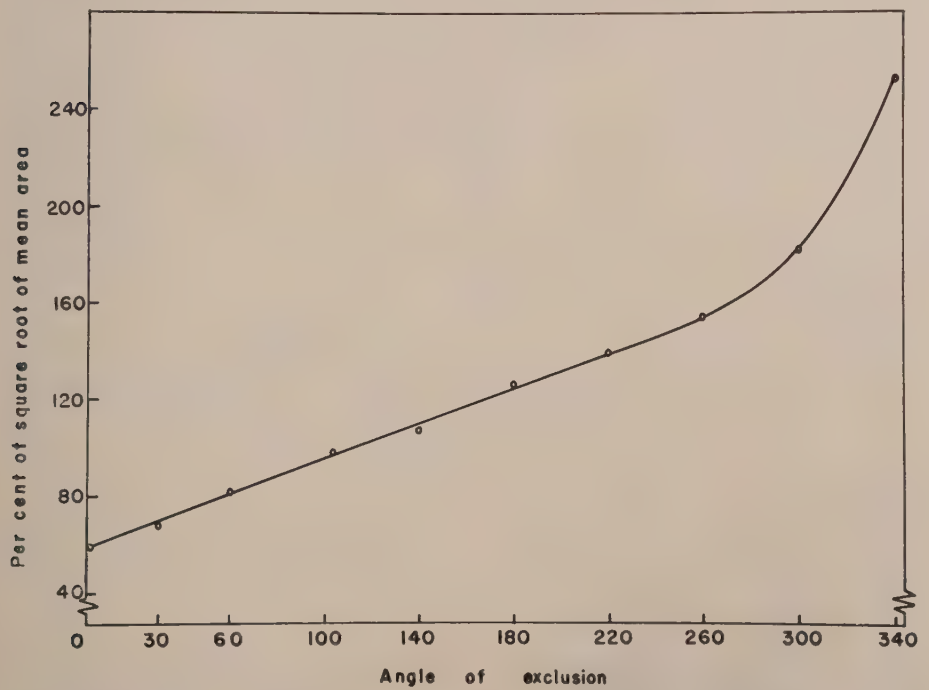

FIG. 4. Distances, expressed as per cent of the square root of the population mean area, obtained through the use of several angles of exclusion with the random pairs method. The increase of distance with increase of angle is approximately linear, except for the 2 largest angles used.

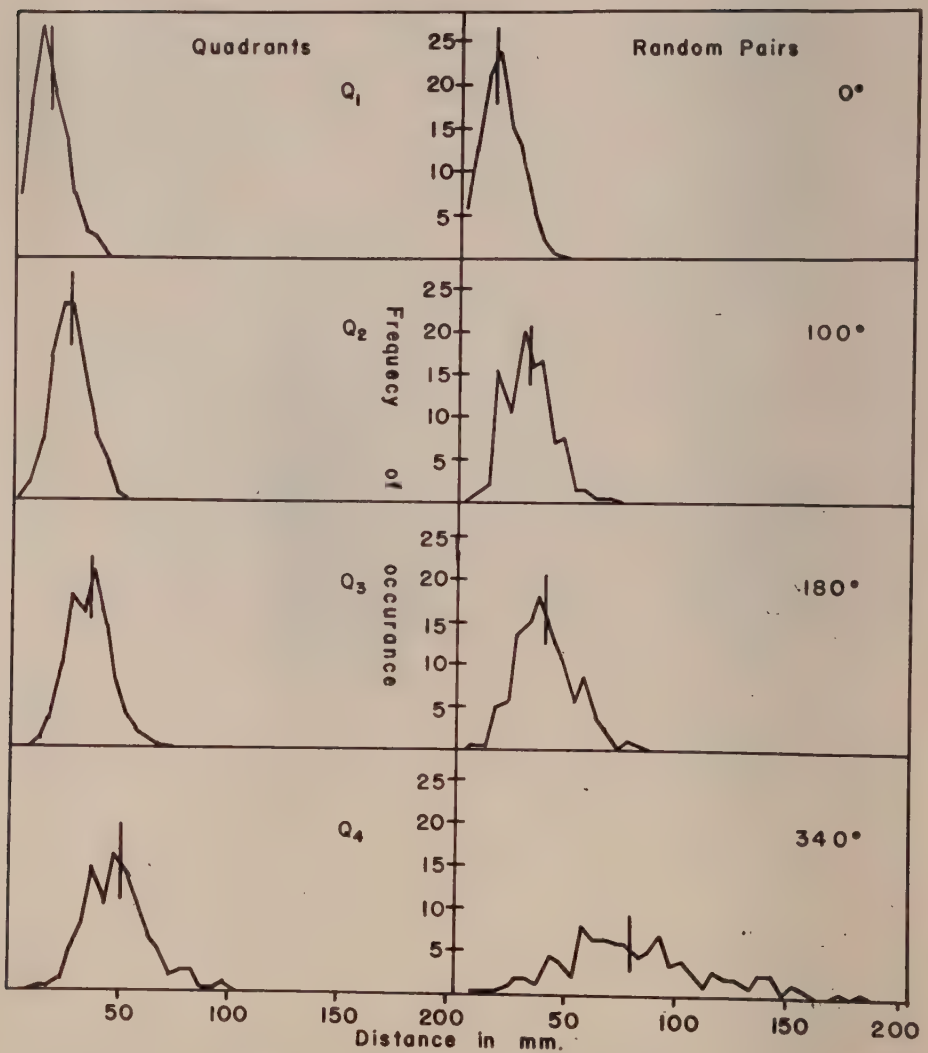

FIG. 5. Frequency polygons of the distances obtained for the 4 quadrants, and for the random pairs method using 4 selected angles of exclusion.

the absence of a left hand tail. The curve is truncated—cut off on the left hand side. What there is of it appears to be symmetrical. Q_2 looks much like Q_1 except that it is moved to the right and the missing tail has been added. It is approximately symmetrical. Q_3 and Q_4 are increasingly skewed to the right. Except for the truncated nature of the curve for the 0 degree angle, there is little indication that the random pairs distributions show a similar increase in skewness with increasing angle of exclusion.

Discussion and Conclusions

The investigation reported in this paper was conducted for the purpose of ascertaining some of the characteristics of a random population. An artificial popu-

lation was used since such a population is free from most of the uncontrollable, and often unknown factors that cause peculiarities in plant distributions in the field. In a sense, this population represents an idealized and simplified map of the plants in a community. It was felt that a knowledge of such an idealized community would be of value as a standard with which existing plant communities could be compared. The results have been discussed as they have been presented. There remains a discussion of the applications of the information herein contained to results obtained by plant ecologists in the field.

Relative density

The accuracy of relative density measurements of random populations appears to be dependent on the number of individuals sampled regardless of the method used to sample the individuals. A minimum of 30 individuals of any species is necessary before any statement can be made regarding its relative density in the population. In terms of usual field practice in forest sociology with the common 10 meter by 10 meter quadrat, only those species with a frequency of 26 per cent or more in a sample of 100 quadrats can be used for accurate statements of relative composition. With only 50 quadrats, this lower limit should be 45 per cent, while with the low number of 25 quadrats the frequency limit should be 70 per cent. The only recourse for species below these limits is to increase the number of quadrats, since an increase in size is not usually practicable in the field. Use of the exclusion angle methods discussed in this paper are subject to the same limitations, and with these methods the only possible way to increase the number of individuals is an increase in number of sampling points, since the number of individuals measured at each point is fixed.

In stands with one or two dominants, as in boreal conifer forests and certain deciduous forests of north temperate regions, the usual sample of 25 to 100 quadrats should give an accurate picture of species composition of the common trees and, since these make up the great preponderance of the individuals present, the lesser species will be rather narrowly defined as well. It does not make much difference in the characterization of a community whether some rare species is listed as having 2 per cent relative density or 4 per cent, although the error, so far as that particular species is concerned, may be very great. When the number of dominants increases, as in the southern Appalachians, then the size of the sample must increase proportionately. No fixed statements as to the size of the sample are now possible but it would appear that quantities approaching the upper feasible limit might be needed. In the tropical rain forests, with 60 to 90 species per hectare (Black, *et al.* 1950) the number of quadrats or points needed for even reasonable accuracy becomes impossibly great. The commonly employed method of using a 100% sample on an area as large as 2 or 3 acres is exceedingly time-consuming, but in spite of this, is still not very precise. This failure of the usual sampling methods to give accurate determinations of such a basic, simple characteristic as relative composition is no doubt responsible for the emphasis placed by the tropical ecologists on physiognomic classification (Beard 1944, Richards 1952).

Area density

Since quadrats are area samples, their use to measure density per unit area is relatively simple. In spite of the simplicity of the quadrat method, its use in the field is both tedious and time-consuming. The number of trees encountered in one 10 by 10 meter quadrat averages four or less in most upland deciduous forests of temperate regions. The amount of work required to lay out such a quadrat with any degree of ac-

curacy is much greater than that required to measure four trees by either of the exclusion angle methods discussed in this paper. In terms of sample size. the angle methods are capable of yielding greater returns per man hour than is the quadrat method. One of the disadvantages of the angle methods is that they have not been the subject of much study and their potentialities and characteristics are not well-known. The results presented in this paper show that distance measurements obtained through the use of these methods follow predictable patterns. The average of the four distances obtained at each point with the quadrant method is very close to the square root of the population mean area. To convert these distances to density per unit area, it is necessary only to square the average distance and divide the result into the number of square feet being used as the unit area. In the case of the random pairs method, average distances have been shown to increase with an increase in the angle of exclusion. This increase is linear over a wide range of exclusion angles, varying from 58 per cent of the square root of the population mean area with no angle of exclusion to 155 per cent with an angle of exclusion of 260 degrees. Any angle throughout this range may be used for field work, although angles of exclusion less than 100 degrees yield data with a higher coefficient of variation than do the larger angles. The distances so obtained must be multiplied by the appropriate correction factor to convert them to the square root of the mean area.

One characteristic of random populations which is often overlooked or at least not completely understood by practicing ecologists is the extreme variability that may be encountered. Regardless of the method used, this variation may be so large as to render any conclusions based on small samples greatly in error. Of equal importance is the fact that aggregated populations display even greater variability. Since this variability is inherent in the populations, the only recourse for the student of plant communities is to increase the size of his sample.

Summary

Some of the characteristics of a randomly distributed population were determined by the use of a map containing 1000 individuals located by means of rectangular coordinates taken from a random numbers table. The randomness of the population was checked by comparison with a Poisson distribution and by areal homogeneity tests. The artificial population was sampled by restricted randomization of sampling points and by both area sample methods and exclusion angle methods. In the former there were varying numbers of individuals in constant areas, while in the latter, a constant number of individuals per sample varied in their spacing distances.

Variability of relative density measurements was very great with small samples. Reasonable accuracy was attained when the number of individuals of the species in question exceeded 30 in the total sample. This was true regardless of sampling method and could be achieved by increasing either the number or the size of the sampling units.

Distances between individuals in the random population measured by any of the exclusion angle methods showed a Gaussian frequency distribution, either directly or after simple transformation. The average of all four distances obtained with the quadrant method was within 2 per cent of the parameter distance obtained from the square root of the population mean area. There was a linear increase in distances obtained with increasing exclusion angles in the random pairs method over the range from zero degrees to 260 degrees.

Perhaps the most important characteristic of a random population demonstrated in this paper is the extreme variability

of the results for any of the measures of plant communities studied. This variability is inherent in random populations and its presence necessitates careful planning of sampling procedure to insure that the results obtained by any sampling method approximate the parameters of the population.

The relation of these findings to actual field practice are discussed, with the general recommendation that larger samples than those generally employed are necessary for satisfactory results.

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FOOD AND COVER RELATIONSHIPS OF THE BOBWHITE QUAIL IN EAST-CENTRAL TEXAS[1]

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More or less distinct ecological regions have been recognized in Texas by Bailey (1905), Tharp (1937), and others. These regions have been based upon average yearly temperature and rainfall, soil type, and vegetation composition. Regardless of the diversity and extremes in climate and dominant vegetation in these various regions, the bobwhite quail is found throughout most of the state. *Colinus virginianus taylori* occurs in the Panhandle and North Texas; *C. v. mexicanus* in the eastern portions; and *C. v. texanus* in the South and West.

Extreme drought, predation, parasites, and other ecological constituents of the environment periodically effect quail populations locally throughout the bird's range. However, food and cover, present in sufficient amounts in the right combination, appear to be the basic requirements that control the occurrance of bobwhites in a given area. This two-year study was undertaken in an attempt to evaluate the significance of the available quail foods and cover in the Post Oak Region of east-central Texas, and their importance in limiting quail populations in that region.

The Post Oak Region: This region is situated in the east-central section of the state, extending southward from the Texas-Oklahoma border for a distance of approximately 350 miles and varying in width from 50 to 75 miles. The topography is mostly level to gently rolling, with some steep slopes and hilly areas. Many areas are considerably eroded, largely by gullying. Kirvin (Norfolk group) and Lufkin (Susquehanna group) are the two major types of soils; they are mostly loose, light-colored sandy loam topsoils with a subsoil of clay and sandy clay.

The average annual rainfall varies between 35 and 40 inches; the average length of the growing season is approximately 250 days. Almost three-fourths of the area is in pastureland that is used primarily by cattle. Cotton, which normally occupies about two-thirds, and corn, occupying about one-fifth, of the cultivated area, with a small acreage of hay and other forage crops, make up the cropping systems on the majority of farms in the area (Bonnen and Thibodeaux 1937).

The post oak (*Quercus stellata*) and the black-jack oak (*Quercus marilandica*) are the two principal dominant species in the upland areas. Several other woody species are often found growing in association with them, of which hackberry (*Celtis occidentalis*), water oak (*Quercus nigra*), overcup oak (*Quercus lyrata*), pecan (*Hicoria pecan*), and black hickory (*Hicoria buckleyi*) are common.

Stands of yaupon (*Ilex vomitoria* and *I. decidua*), dogwood (*Cornus florida*), winged elm (*Ulmus alata*), and occasionally others often form a dense understory in much of the post oak woodlands. The following species are also commonly found singly in open areas, along streams, and in thickets: wild plum (*Prunus mexicana*), honey locust (*Gleditsia triacanthos*), hawthorn (*Crataegus spathulata* and *C. marshalli*), prickly ash (*Xanthoxylum clava-herculis*), sumac (*Rhus copallina*), bois d'arc (*Toxylon pomifer-*

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um), cedar (*Juniperus lucayana*) and sweet gum (*Liquidambar styraciflua*).

The dominant pasture grasses are little bluestem (*Andropogon scoparius*) and silver beardgrass (*A. saccharoides*), grama grasses (*Bouteloua curtipendula* and *B. hirsuta*), panic grass (*Panicum halli, P. obtusum, P. lindheimeri* and *P. texanum*), bull grass (*Paspalum longipilum* and *P. pubescens*), and buffalo grass (*Buchloe dactyloides*) are also common and form a large percentage of the understory grass species. Overgrazing in many areas has drastically changed the grass species composition, and heavy stands of needlegrass (*Stipa leucotricha*), three-awn grass (*Aristida purpurescens, A. oligantha* and *A. intermedia*), broomweed (*Gutierezia texana*), Johnson grass (*Sorghum halepense*), goatweed (*Croton lindheimeri, C. lindheimeranus, C. monanthogymus* and *C. texensis*) and others have become established.

Although large tracts of the Post Oak Region have been opened by clearing operations during the last 25 to 35 years, much of this cleared area is now being reclaimed by brush and woody species. The result is an increased "edge" effect that has been, in many areas, of primary importance for increasing quail numbers by providing additional suitable habitat.

Cover Types

What heights quail population numbers will reach depends primarily upon the quality and quantity of food and cover for a given area and the pattern of distribution of these two essentials. Leopold (1933) points out the various kinds of cover (escape, loafing, nesting and roosting) apparently essential in this habitat. He further states that the "Bobwhite quail . . . probably reached a maximum abundance during that stage of settlement when the composition of their range accidentally reached an equal proportion of brush, woodland, and crude cultivation."

The fact has long been established that the bobwhite is not a species dependent upon a climax vegetation, but rather one that prefers a lower seral stage. A habitat providing the greatest amount of "edge" such as fence rows, draws, and ecotones between woodland and grassland appears to be the most satisfactory. Pastureland that is grazed fairly heavily, to the point where goatweed, partridge pea (*Cassia fasciculata*), and many other annual weed species appear, provides the best local quail habitat conditions in the Post Oak area when combined with rose (*Rosa bracteata*), stretchberry (*Smilax bona-nox*), winged elm, and yaupon thickets.

The Post Oak Region of Texas contains a great variety of local habitat types, differing in extent and in vegetation composition. The existing cover types today are directly or indirectly dependent upon past and present land-use practices. It is difficult to separate completely the cover types into exact categories and to evaluate them as food, nesting, escape, travel, or headquarters cover. On the basis of vegetation composition and life form, however, the vegetation types utilized by the bobwhites in this central Post Oak belt for food and/or cover can be arbitrarily divided into three main groups: brush thickets, grassland, and woods edge. This grouping is not exact by any means, because there is often an intergradation of one type into another. For example, difference between woods' edge and brush is often slight, since the brush may represent merely a young growth stage of the woodland type.

Stretchberry is one of the most satisfactory native plants providing protective cover for bobwhites in this region. It occurs commonly throughout the area, growing rapidly and forming thick tangles, and is especially adapted to climbing, often growing up into the tree branches to a height of 20 to 30 feet. Although it is a strong competitor for available space, other plants such as hawthorn, winged elm, oak saplings, and yaupon are able to survive and grow in the same thicket. Occasionally stretchberry invades a previously established thicket of yau-

pon, plum, or hawthorn and forms a canopy that provides exceptionally good quail cover. Wild grape, *Vitis candicans,* growing in similar fashion, also supplies good cover.

The woods' edge provides both food and cover at certain periods of the year, but its value to bobwhites is limited, depending upon certain combinations of ecological factors. In many localities, the line separating pasture from woods is sharp. When oak exists in almost pure stands, its value to quail is greatly reduced. Normally, however, the woods' edge, to an approximate depth of 50 yards, is comprised of oak, yaupon, stretchberry, rattan (*Berchemia scandens*), French mulberry (*Callicarpa americana*), and other woody species. Cover of this type often constitutes a sizable portion of a covey range, and bobwhites use it for protection and, in years of high oak mast production, as an area in which to feed.

Brush thickets and woods' edges supply cover and protection to wintering bobwhite coveys, but the nesting and summer birds are dependent primarily upon the grass cover for protection. Pastures and grasslands provide, in addition to cover, a yearly food supply, thereby constituting the two essentials in the bobwhites' habitat. Dense stands of little bluestem and silver beardgrass comprise cover most suited for nesting birds as well as for those seeking ground cover for protection. Grazing pressure is of prime importance in affecting the vegetative composition of pastures. Pastures under careful management often contain a high percentage of bluestem grasses, while needlegrass, three-awn grass, and a large number of annual weeds appear with overgrazing.

During summer, the roadsides are occupied by nesting bobwhites, pairs, and single cock birds. Silver beardgrass is the dominant grass species along many of the highways, although Johnson grass occurs in dense stands in many localities. Sunflowers (*Helianthus annus*), thistle (*Cirsium discolor* and *C. virginianum*), goatweed, and other annual weeds growing along roadsides furnish good cover and a source of food to those birds inhabiting such areas.

Areas surrounding water tanks, stock barns, holding pens for livestock, and Negro cabins are often trampled or heavily overgrazed. In such locations, ragweed (*Ambrosia artemisiifolia*), broomweed (*Gutierrezia texana*), dock (*Rumex pulcher*), marsh elder (*Iva ciliata*), and others persist in dense stands. These, however, provide winter food as well as some cover in summer.

Food Relationships

Judd (1905) was one of the first workers to study the problem of food requirements of quail. Since that time, Stoddard (1931), Martin (1935), Davison (1940, 1942), Errington (1939), and others have added substantially to the knowledge of food habits and foods of bobwhites. Lee (1948) and Baumgartner (1945) investigated the food habits of bobwhites in Oklahoma, while Lehmann (1937) and Wagner (1949) studied the food requirements of quail in Texas. During 1950 and 1951, an attempt was made to determine from crop and gizzard analyses the yearly food habits of bobwhites in the Post Oak Region.

Methods of Crop Analyses: Through the cooperation of local hunters, 185 crops and 222 gizzards were collected in the 1950-51 hunting season (December 1-January 16) and 361 crops and 487 gizzards in the 1951-52 season. Since all crops and viscera were preserved in 4 per cent formalin, it was necessary to open them and dry the contents. They were then placed in 3" x 5½" cellophane bags, properly labeled, and filed until time permitted analysis of the sample. Between February 1 and November 30, 1951, 32 bobwhites were collected for food habits study. Based on crop analysis, the volume, percentage of volume, and frequency of occurrence of summer foods are listed by months in Table I.

TABLE I. Analysis (by months) of Food Eaten by 32 Bobwhites Collected Between February 1 and November 30, 1951.

	Volume in cc.	Percentage By Volume	Frequency of Occurrence
February—6 crops			
Quercus sp.	2.0	51.28	2
Croton spp.	1.5	38.46	4
Green Vegetation	.2	5.12	6
Strophostyles leiosperma	.1	5.12	2
Aristida sp.	Tr	....	2
Scleria ciliata	Tr	....	2
Galactia regularis	Tr	....	1
Cassia fasciculata	Tr	....	1
Paspalum sp.	Tr	....	1
Animal matter	Tr	....	1
	309	99.98	..
March—9 crops			
Croton spp.	8.8	62.41	8
Quercus spp.	2.5	17.73	3
Bumelia lanuginosa	.9	6.38	1
Panicum sp.	.5	3.54	5
Animal matter	.5	3.54	3
Green vegetation	.3	2.12	3
Paspalum sp.	.2	1.41	4
Carex sp.	.2	1.41	2
Vicia sp.	.1	.70	1
Galactia regularis	.1	.70	1
Lespedeza sp.	Tr	....	2
Sorghum halepense	Tr	....	1
Rumex sp.	Tr	....	1
Scleria ciliata	Tr	....	1
Strophostyles leiosperma	Tr	....	1
Heterotheca subaxillaris	Tr	....	1
	14.1	99.84	..
April—4 crops			
Croton spp.	3.0	38.46	1
Green vegetation	2.9	37.17	4
Quercus sp.	1.1	14.10	1
Euphorbia bicolor	.3	3.84	1
Serinia oppositifolia	.2	2.56	1
Animal Matter	.2	2.56	2
Helianthus sp.	.1	1.28	1
Panicum sp.	Tr	....	1
Cassia fasciculata	Tr	....	1
	7.8	99.97	.
May—3 crops			
Panicum sp.	7.3	54.07	3
Animal matter	4.5	33.33	2
Green vegetation	.5	3.70	2
Paspalum sp.	.3	2.22	2
Croton sp.	.3	2.22	2
Euphorbia bicolor	.2	1.48	1
Carex sp.	.2	1.48	1
Oenothera sp.	.1	.74	1
Vicia sp.	.1	.74	1
	13.5	99.98	..
June; July—3 crops			
Animal matter	3.0	34.48	2
Panicum spp.	2.7	31.03	2
Zea mays	1.8	20.68	1
Croton spp.	.8	9.08	3
Panicum texanum	.2	2.30	1
Euphorbia bicolor	.1	1.14	1
Paspalum sp.	.1	1.14	1
Vicia spp.	Tr	....	2
Green vegetation	Tr	....	2
	8.7	99.85	..
August—4 crops			
Animal matter	5.7	44.18	4
Croton spp.	3.9	30.23	4
Panicum sp.	1.6	12.40	3
Zea mays	1.1	8.52	1
Vicia sp.	.4	3.10	3
Euphorbia bicolor	.1	.77	1
Panicum texanum	.1	.77	1
Green vegetation	Tr	....	1
Scleria oligantha	Tr	....	1
Paspalum sp.	Tr	....	1
Scleria ciliata	Tr	....	1
Smilax sp.	Tr	....	1
	12.9	99.97	..
Sept.; Oct.; Nov.—4 crops			
Croton spp.	6.5	69.14	4
Oenothera sp.	1.5	15.96	1
Sorghum halepense	.6	6.38	1
Animal matter	.4	4.26	2
Avena sp.	.2	2.13	1
Paspalum sp.	.1	1.06	1
Strophostyles sp.	.1	1.06	1
Cassia fasciculata	Tr	....	1
Cathartolinum virginianum	Tr	....	1
Andropogon sp.	Tr	....	1
Green vegetation	Tr	....	2
	9.4	99.99	.

Martin, Gensch and Brown (1946), and Davison (1940) discussed and evaluated the various techniques of analyzing game bird foods. The volume summation method described by Martin *et al.* was followed to some extent in analyzing the crops collected in this study. Each crop was measured separately. All seeds and plant material were identified by comparison with herbarium specimens and with fresh material collected in the fields. A. C. Martin, Patuxent Research Refuge, Laurel, Maryland, and F. H. Wagner, University of Wisconsin, Madison, identified some seed material. Volumetric measurements were made by sand displacement, using very fine sand (250-105 microns, easily passing through a 0.500 mm. sieve) as follows:

Each component species of each crop

was measured separately by mixing the seeds or other food material with a known volume of sand. The seeds were first placed in a 15-cubic centimeter glass centrifuge cylinder graduated to 0.10 cubic centimeter, to which the known volume of sand was added. By using a teasing needle and tapping the cylinder, the sand was thoroughly mixed with the seeds so that no spaces or pockets remained. A reading was taken to the nearest 0.10 cc. The mixture was then sifted through a piece of 60-mesh brass screen which again separated the seeds from the sand. The known volume of displacement sand was remeasured after each four crops because a small amount of sand occasionally adhered to seeds or was lost during the sifting operation. The total volume of each component food item was tabulated, and from the final volumetric total the percentage of each item was computed. The volumes, percentages, and frequency of occurrence of each item in crops collected during the 1950-51 and 1951-52 hunting seasons are listed in Tables II and III.

Results of stomach analysis: The two principal winter food items eaten by quail in this area, as determined by crop and gizzard analyses, are acorns and goatweed. Depending upon seasonal climatic variations and local habitat differences in vegetation composition, the following species of plants may also be considered important sources of food to the bobwhite in East-central Texas: Texas millet, panic grass, ragweed, Johnson grass, wild bean, snow-in-the-mountain, elm and sunflower.

The various species of panic grass are significant since they constitute one of the earliest seeders in the spring. These grasses are often taken by bobwhites while still in seed heads, and they provide some relief from the late winter shortage of food. Lehmann and Ward (1941) classify several species of *Panicum* as important food items in the diet of bobwhites of southwestern Texas. Wagner (1949) found *Panicum* to be of no particular importance as a food of North Texas bobwhites, but his samples were limited in periods collected and in numbers.

Bobwhites utilized seeds of several species of legumes, particularly *Strophostyles, Galactia,* and *Rhynchosia,* although the last two were never taken in appreciable amounts. Stoddard (1931) found beggarweed, *Desmodium* spp., second in importance to lespedeza (the most important legume eaten) in the Southeast. In the Post Oak area, however, this item is of little importance and forms but a small percentage of the food eaten.

Yellow corn (*Zea mays*), lespedeza, and, to a limited extent, cowpeas (*Vigna sinensis*) rated high in the total volume of foods eaten, but their frequency of occurrence was low. A few birds with crops containing corn, lespedeza, or other cultivated plant seeds were misleading until final tabulations were made to determine the most important foods eaten by quail.

For example, cowpeas (Table II) were classified as fifth in importance, yet they occurred in only seven of the 185 crops examined. Simularly, corn ranked eighth in importance in birds examined during the 1950-51 season, although only 6 quail crops contained this food. Corn was listed as the fifth most important food item in birds collected in the 1951-52 quail season, but it occurred in only 12 crops.

Fallow fields of corn, cotton, sorghum, and other cultivated crops often provide an excellent source of food for bobwhites, both from the cultivated plants and the weed species that occur in them. Goatweed, Johnson grass, paspalum, and many other plants form a source of winter foods and, to a more limited extent, protective cover while the quail are feeding. Goatweed and other weeds form luxuriant stands on soil disturbed by plowing or disking. By plowing strips around or beside cover utilized by quail, it is possible to supply a good source of natural food with a minimum of time and cost.

Panicum spp., *Croton* spp, and animal matter were the three most important nat-

TABLE II. Analysis of Foods Eaten by 185 Bobwhites collected from 11 Counties in the Post Oak Section of Texas, December 1, 1950-January 16, 1951.

Species	Volume in cc.	Percentage By Volume	Frequency of Occurrence
Quercus spp. (Acorns)	118.8	39.71	89
Croton spp. (Goatweed)	45.2	15.11	99
Ulmus sp. (Elm)	24.8	8.29	39
Lespedeza spp. (Common, Korean, Wild)	24.7	8.25	41
Vigna sinensis (Cowpea)	15.2	5.08	7
Ambrosia spp. (Ragweed)	14.4	4.81	47
Sorghum halepense (Johnson Grass)	7.9	2.64	25
Zea mays (Corn)	7.6	2.54	6
Panicum spp. (Panic Grass)	6.4	2.13	54
Sorghum vulgare (Sorghum)	3.2	1.06	10
Animal matter	2.9	.96	34
Iva spp. (Marsh Elder)	2.9	.96	18
Panicum texanum (Texas Millet)	2.4	.80	9
Euphorbia bicolor (Snow-on-the-Mountain)	2.3	.76	9
Green vegetation	2.2	.73	53
Liquidambar styraciflua (Sweet Gum)	2.1	.70	2
Cassia fasciculata (Partridge Pea)	2.0	.66	18
Desmodium spp. (Beggar's Tick)	1.8	.60	23
Paspalum spp. (Bull Grass)	1.7	.56	42
Strophostyles spp. (Wild Bean)	1.7	.56	38
Bumelia spp. (Woolly Buckthorn)	1.0	.33	3
Maclura pomifera (Bois d'Arc)	.9	.30	5
Unidentified spp.	.9	.30	11
Cissus arborea (Peppervine)	.8	.26	12
Rhus spp. (Sumac)	.8	.26	6
Avena sativa (Oats)	.7	.23	3
Amaranthus sp. (Pigweed)	.6	.20	4
Symphoricarpos orbiculatus (Coralberry)	.6	.20	6
Galactia regularis (Milk Pea)	.5	.16	13
Paspalum floridanum (Florida paspalum)	.5	.16	3
Sesbania exaltata (long-podded Sesban)	.4	.13	3
Strophostyles helvola (Trailing Wild Bean)	.2	.06	2
Helianthus spp. (Sunflower)	.2	.06	5
Heterotheca subaxillaris (Camphor Weed)	.2	.06	6
Scleria ciliata (Hairy Nut-rush)	.2	.06	4
Campsis radicans (Trumpet Creeper)	.2	.06	2
Scleria oligantha (Few-flowered Nut-rush)	.1	.03	1
Panicum fasciculatum (Browntop Paspalum)	.1	.03	2
Artistida spp. (Three-awn Grass)	Tr	...	8
Rhynchosia latifolia (Prairie Rhynchosia)	Tr	...	1
Rumex sp. (Dock)	Tr	...	3
Carex sp. (Sedge)	Tr	...	3
Uniola laxa (Slender Spike-grass)	Tr	...	2
Andropogon sp. (Beard-grass)	Tr	...	2
Parthenocissus sp. (Virginia Creeper)	Tr	...	1
Ilex vomitoria (Yaupon)	Tr	...	1
Plantago sp. (Plantain)	Tr	...	1
Cathartolinum virginianum (Wild Flax)	Tr	...	1
Vicia sp. (Vetch)	Tr	...	1
	299.1	99.70	..

ural foods eaten by bobwhites in this region during late spring, summer and early fall in 1951. Grasshoppers (Acrididae and Tettigoniidae), stink-bugs (Pentatomidae), leaf-hoppers (Cicadellidae), and cucumber beetles (Chrysomelidae) constituted most of the animal matter consumed. Snails were occasionally taken, but usually in small quantities. The only notable exception was an adult female bobwhite, collected in Brazos County, on May 24, 1951, the crop of which contained 14 snails, comprising one-eighth of the total volume of food.

TABLE III. Analysis of Foods Eaten by 361 Bobwhites collected from 13 Counties in the Post Oak Section of Texas, December 1, 1951-January 16, 1952.

Species	Volume in cc.	Percentage By Volume	Frequency of Occurrence
Croton spp. (Goatweed)	453.2	72.18	324
Panicum texanum (Texas Millet)	43.0	6.84	37
Euphorbia bicolor (Snow-on-the-Mountain)	22.1	3.52	29
Sorghum halepense (Johnson Grass)	21.7	3.45	41
Zea mays (Corn)	15.5	2.46	12
Helianthus spp. (Sunflower)	14.3	2.21	19
Ambrosia spp. (Ragweed)	13.2	2.10	41
Green vegetation	5.6	.89	214
Animal matter (Insects, Snails, etc.)	5.1	.81	65
Bumelia spp. (Woolly Buckthorn)	4.1	.65	12
Ulmus sp. (Elm)	3.4	.54	9
Sorghum vulgare (Sorghum)	3.2	.50	6
Quercus spp. (Acorn)	2.9	.46	6
Vigna sinensis (Cowpea)	2.3	.36	3
Strophostyles helvola (Wild Bean)	2.0	.31	8
Celtis occidentalis (Hackberry)	2.0	.31	16
Strophostyles spp. (Wild Bean)	1.9	.30	49
Cassia fasciculata (Partridge Pea)	1.9	.30	61
Galactia regularis (Milk Pea)	1.3	.20	13
Forestiera neomexicana (Adelia)	1.2	.19	5
Iva spp. (Marsh Elder)	1.2	.19	5
Vicia spp. (Grape)	1.0	.15	15
Commelina erecta (Dayflower)	.8	.12	10
Panicum spp. (Panic Grass)	.8	.12	22
Paspalum spp. (Bull Grass)	.8	.12	40
Scleria ciliata (Nut-rush)	.8	.12	3
Rhynchosia latifolia (Peavine)	.5	.07	7
Lespedeza spp. (Lespedeza)	.2	.03	14
Heterotheca subaxillaris (Camphor Weed)	.2	.03	23
Geranium carolinianum (Cranesbill)	.2	.03	6
Digitaria sp. (Crabgrass)	.2	.03	8
Amaranthus sp. (Pigweed)	.2	.03	2
Cissus arborea (Peppervine)	.2	.03	2
Rumex spp. (Dock)	.2	.03	4
Aristida spp. (Three-awn Grass)	.2	.03	53
Paspalum floridanum (Large-seeded Paspalum)	.1	.01	2
Toxicodendron radicans (Poison Ivy)	.1	.01	3
Prosopis chilensis (Mesquite)	.1	.01	1
Callicarpa americana (French Mulberry)	.1	.01	1
Carex spp. (Sedge)	Tr	...	3
Diodia teres (Poor Joe)	Tr	...	7
Cathartolinum virginianum (Wild Yellow Flax)	Tr	...	11
Jacquemontia tammifolia (Morning Glory)	Tr	...	2
Uniola laxa (Slender Spike-grass)	Tr	...	1
Bouteloua sp. (Grama Grass)	Tr	...	1
Avena sativa (Oats)	Tr	...	1
Desmodium sp. (Beggar's Tick)	Tr	...	2
Andropogon spp. (Beard-grass)	Tr	...	4
Sesbania exaltata (Long-podded Sesban)	Tr	...	1
Symphoricarpos orbiculatus (Coralberry)	Tr	...	1
Melilotus sp. (Sweet Clover)	Tr	...	1
	627.8	99.75	

This bird was in the process of completing a clutch of eggs. Green vegetation was consumed in all months of the year.

Monthly ground seed samples were taken in typical bobwhite habitat in order to obtain an estimate of the type and amount of food actually available to the quail throughout the year. Seeds were removed from 15 square feet (15-one square foot samples) in pasture, woods' edge

and brush thickets, and the number and species found were recorded.

As determined by these samples (Robertson County) and field observations of blooming and seeding periods, a few species of plants produced large and lasting seed crops that were seldom utilized by bobwhites. Stretchbeery and yaupon berries were available to them in brush and woody edges throughout the year, and poor Joe seeds (*Diodia teres*) were common in pastures and waste places each month. These items were seldom eaten, however.

Gizzard analyses (percentage estimate of each food item in each gizzard) showed a higher frequency of occurrence of yaupon than was evident in the crops. Apparently this is due in part to the resistance of these hard seeds to the grinding effect of the gizzard. In several instances, it was observed that some yaupon seeds in a particular gizzard varied from others in the degree to which they had been reduced by grinding, thus representing the remnants of two or possibly more previous feedings. This situation was also noticeable in other hard seeds such as Sedge (*Scleria* spp.), sumac (*Rhus* spp.), coralberry (*Symphoricarpos orbiculatus*), and French mulberry (*Callicarpa americana*).

Most of the feeding is done in open pastures and fields. Field observations of quail feeding, and the results of crop and gizzard analyses, indicate that brush thickets and woody edges are of little importance as a source of food except in years of high oak mast production. Thickets and other areas of dense woody vegetation function principally as escape or loafing cover and are of only secondary importance as sources of food.

There is a tendency on the part of bobwhites to change their diet when the availability of food changes. When several grasses, especially *Panicum,* produced seed in early spring, quail began utilizing them. Insects and green vegetation were taken in large quantities as they became available in late spring and summer. There appear to be three periods (fall and winter—seeds, spring—green vegetation and summer—insects) in which distinct types or groups of food species appear and are utilized by quail. However, considerable variation and overlap occur within each year and from one year to the next.

Results of the food habits study during 1950 and 1951 showed that a large variety of foods were consumed. However, plants belonging to four families (Euphorbiaceae, Leguminosae, Gramineae, and Fagaceae) produced seeds most valuable to bobwhites, and they constituted the most important source, by number and volume, of all the foods consumed by them.

Food Competitor Species

Food and cover are basically the two most important habitat requirements in the life of a bobwhite quail, and the quantity and quality of each in a particular area will determine, at least in part, the number of quail that occupy that area. Cover in most areas within the central Post Oak Region appears to be sufficient to maintain relatively high quail populations, and apparently little if any competition for it exists between bobwhites and other species.

An endeavor was made during this study to determine the significance of certain birds and mammals as potential food competitors of the bobwhite. Several species of song birds common in this region were collected in Robertson and Brazos counties between October 1 and May 1, 1951. The results of the stomach analyses of these species are recorded in Table IV.

Song Birds as Food Competitor Species: The southern half of the United States serves as a wintering ground for thousands of migrating birds. In the central Post Oak Region, large numbers of sparrows, towhees, field larks, cardinals, thrashers, woodpeckers, blackbirds, blue jays, robins, and many other species arrive during September and October each year. Some individuals of most of these species are permanent residents, although

TABLE IV. Results of Stomach Analyses of Seven Species of Songbirds Collected in Brazos and Roberson Counties, Texas. October 1950 through April 1951.

Food Species	*Mimus polyglottus* Mockingbird (30 stomachs)		*Toxostoma rufum* Brown Thrasher (19 stomachs)		*Turdus migratorius* Robin (7 stomachs)		*Sturnella neglecta* Meadowlark (46 stomachs)		*Richmondena cardinalis* Cardinal (33 stomachs)		*Cyanocitta cristata* Blue Jay (10 stomachs)		*Molothrus ater* Cowbird (9 stomachs)	
	Total Vol. cc	% by Vol.	Total Vol. cc	% by Vol.	Total Vol. cc	% by Vol.	Total Vol. cc	% by Vol.	Total Vol. cc	% by Vol.	Total Vol. cc	% by Vol.	Total Vol. cc	% by Vol.
Insect matter	19.3	57.52	9.8	38.58	1.7	18.88	37.7	73.20	12.7	58.52	8.2	50.00	.4	8.89
Vegetable matter	.4	1.18	.8	3.15	.3	3.33	5.9	11.47	8.8	40.55	.3	1.83	1.7	37.78
Toxicodendron radicans	.2	.59	.7	2.76	...	...	...	...	.1	.46				
Celtis occidentalis	.2	.59	.4	1.57										
Smilax sp.	.6	1.77	.1	.39										
Callicarpa americana	1.0	2.95												
Ilex sp.	8.1	23.90	...	...	6.4	71.11								
Xanthoxylum clava-herculis	.3	.88												
Berchemia scandens	.1	.29												
Viburnum rufidulum	.8	2.36												
Vaccinium arboreum	.1	.29												
Carex sp.	.5	1.47	...	...	...	...	Tr	...	...	...	...	...	Tr	
Cornus sp.	1.7	5.01												
Cissus arborea	.4	1.18												
Cocculus carolinus	...	...	.5	1.97										
Quercus sp.	...	...	11.2	44.10	...	...	...	...	...	...	7.9	48.17		
Symphoricarpos orbicularis	...	...	.1	.39										
Snails	...	...	1.8	7.09										
Andropogon sp.	...	...	...	...	...	...	1.7	3.30	.1	.46	...	...	.5	11.11
Digitaria sp.	...	...	...	...	...	...	.1	.19						
Vicia sp.	...	...	...	...	...	...	.1	.19						
Sorghum halepense	...	...	...	...	...	...	.6	1.17						
Croton spp.	...	...	...	...	...	...	.1	.19						
Helianthus sp.	...	...	...	...	...	...	.4	.78						
Panicum spp.	...	...	...	...	...	...	1.0	1.94	...	...	...	...	.7	15.56
Zea mays	...	...	...	...	...	...	.5	.97	...	...	...	...	.6	13.33
Sorghum vulgare	...	...	...	...	...	...	.8	1.55						
Rumex sp.	...	...	...	...	...	...	Tr							
Panicum texanum	...	...	...	...	...	...	2.6	5.05	...	...	...	...	.5	11.11
Juniperus sp.	...	...	...	...	.6	6.67								
Avena sp.	...	...	...	...	...	...	...	...	...	...	...	...	.1	2.22
Totals	53.9	99.97	25.4	99.99	9.0	99.99	51.5	99.98	21.7	99.99	16.4	100.00	4.5	99.98

the population of each is greatly increased during the winter months. Approximately 200 birds were collected between October 1, 1951, and May 1, 1951, and examined in an attempt to determine the relative importance of each species as a competitor of the bobwhite for the available food.

Table IV includes several of the species collected, the number examined, and the food items consumed by them. The number of each species collected is not large, but it is believed sufficient to serve as an index of their winter food habits in this region. Stomach analyses were conducted in a manner similar to that of the quail crops.

Consideration must be given to the abundance of each species and their method of feeding as well as to the actual kind and amount of food consumed. Of all the birds considered during this study, the meadowlark and mourning dove are closest to the bobwhite in feeding habits. All three species are ground feeders and utilize open pastures and fields in seeking the greater portion of their food supply.

The mourning dove appears to be a possible natural avian food competitor of the quail. Several dove hunters contacted during the hunting season reported goatweed as the principal food encountered in the crops of these birds. Eight dove crops examined by the author in

October of 1950 contained large numbers of goatweed (average 187 seeds per crop) and *Panicum* seeds. However, doves are highly mobile and are not dependent upon a limited area in which to feed. They are able to feed in open, exposed areas devoid of nearby cover so necessary to bobwhites, thus reducing the amount of competition that might exist between them and quail.

Meadowlarks feed in a manner similar to bobwhites, but they are more mobile, do not concentrate all of their feeding activities in one localized area, and forage on the roadsides more frequently. Normally roadsides are little utilized by winter coveys of quail, so that other birds feeding there are not competing with them. Insect matter was the most important food item consumed by meadowlarks; seeds (those that were also eaten by bobwhites) were taken in very small amounts. Although meadowlarks are numerous in this region in winter, slight competition between them and the bobwhites was revealed in this study. It is possible, however, that in years of critical shortages of food they may be serious competitors.

Lay and Siegler (1937) have discussed the value of blue jays in making acorns available to bobwhites. Apparently the number of acorns consumed by the jay is more than compensated for by the particles (and whole acorns) dropped while feeding. Many of these acorns are then utilized by bobwhites. Acorns were also consumed by the brown thrasher, although insect matter rated highest as a food item eaten by both the jay and the thrasher. The amount of mast consumed by these species is insignificant when compared with the total produced and with that eaten by other species, particularly by raccoons, deer, and other mammals.

Mockingbirds removed much of their food directly from the trees or shrubs. They fed to a considerable extent on insects, although seeds (whole fruits) of hackberry, poison ivy, stretchberry, yaupon, and French mulberry were taken. Several foods eaten by mockingbirds are also consumed by quail but not in large quantities, and apparently little competition for available foods exists between these species.

Identification of food items eaten by cardinals was limited because a large percentage of the food is crushed by the bill before it passes directly into the stomach. The term vegetable matter was applied to green vegetation, portions of seeds and partially digested material not identified. Insects constituted the major food eaten by cardinals, and seeds of poison ivy, grasses, and other plants were taken in small quantities. The available data indicate little or no competition for food between cardinals and quail. All of the seeds and fruits eaten by the various song birds examined in this study, with the exception of acorns, were taken by bobwhites in very small amounts.

Meadowlarks, mockingbirds, brown thrashers, robins, cardinals, and many other song birds utilize insects whenever possible, supplementing this diet with various fruits and seeds. Normally insects are available at all seasons in this region, although they are naturally more numerous during the summer months. Birds that had been utilizing fruits and seeds during the winter months quickly changed to insects when they became more abundant in March of 1951. Observations of feeding habits, kinds of food eaten, and abundance of the various birds in the Post Oak Region indicate that song birds and doves are apparently of little or no significance in competing with bobwhites for the available natural food supply.

The above conclusion, however, may have one noteworthy exception. Migrating flocks of certain species of birds may stop temporarily in an area and consume a large part of the available food. This occurrence has been previously pointed out in regard to the mourning dove, and it also has been observed in the case of the bronzed grackle (*Quiscalus versicolor*).

On February 26, 1951, a large flock of these grackles, estimated at 500 birds, was noted feeding on the ground in a section of post oak woods bordering the Old San Antonio Road, Brazos County, Texas. Four birds were collected from this flock, and all contained pieces of acorns, averaging 1.4 cc per bird. A flock of birds of this size can remove a large quantity of food and possibly, under certain conditions, remove a large portion of the food that would otherwise be used by bobwhites inhabiting that area.

However, these birds also tend to be rather mobile and to wander considerably over large areas. A similar condition exists with the large flocks of cowbirds that winter or pass through this area in the fall and spring. An exact and even relative measure of the amount of food removed from a given area by birds and other animals is extremely difficult, if not impossible. In regions where they occur, livestock, deer, and domestic fowl account for a certain portion of natural food. A food habits study of the raccoon, the opossum, the gray fox, and the ringtail cat (Wood 1952) showed that these animals also utilize acorns and other seeds and fruits when they became available in this region. All of these forms, as well as the bobwhite, utilize the available food supply in a given area and gradually reduce it.

Food Consumption by Rodents: Rodents were censused on two areas also inhabited by quail in Robertson County in October 1950 and in February, July, and December of 1951. All rodents were live-trapped, toe-clipped for identification, and released. Small metal live traps, baited with dry oatmeal, were used. These were set along two transect lines 400 feet apart; the traps were spaced at 20-foot intervals. The census was continued for three days on each area. Periodic censusing of rodents on these areas was conducted in an attempt to determine the relative number of rodents in a typical section of pasture utilized by quail and the general fluctuations in their population numbers.

Numerous workers have studied the food habits of various rodents, and Allen (1894), Blair (1937), and Glass (1946) have added significantly to our knowledge of certain species found in southern United States. In the upland Post Oak Region of Texas, cotton rats (*Sigmodon hispidus*), hispid pocket mice, (*Perognathus hispidus*), harvest mice, (*Reithrodontomys* spp.), and white-footed mice (*Peromyscus* spp.) are common and they frequent the open pastures and fields. Apparently rodents are one of the strongest competitors of bobwhites in this area for certain seeds and other foods. The cotton rat, although common, feeds mostly upon the vegetative portions of various plants (particularly *Andropogon* spp.), and apparently it consumes very few seeds. However, *Peromyscus leucopus, Perognathus hispidus, Reithrodontomys fulvescens,* and *R. montanus,* each also common in this area, consume large quantities of seeds.

To obtain some indication of the number of seeds one of these rodents might consume in a 24-hour period, one animal of each species was kept in the laboratory and fed goatweed seeds (*C. lindheimeri* and *C. monathogamus*). The seeds were counted before being fed to the mice, and all seeds not eaten were accounted for on the following day. Green vegetation was available at all times. This experiment had obvious limitations since the mice were kept under artificial conditions and the number of specimens considered was too small to justify definite conclusions. The data are presented only as a possible index to the quantity of food these species might be expected to consume if an unlimited supply were available to them.

An adult female *Reithrodonthomys fulvescens* consumed an average of 58.3 ± 9.3 goatweed seeds per night during the two-week period. An adult female *Peromyscus leucopus* averaged 95.4 ± 13.1 seeds each night during the same period. An adult female *Perognathus hispidus*

averaged 144 ± 15.4 goatweed seeds each night for a six-day period. Assuming these figures to be reasonably accurate for the species, it becomes obvious that a large number of seeds may be removed by these mice wherever they occur.

Some noteworthy field observations were made concerning the food habits of these rodent species. On April 23, 1951, Robertson County, Texas, a cache of seeds was uncovered at the base of a silver beardgrass clump; probably the seeds were stored by a harvest mouse. The species found and the number of each are as follows: partridge pea, 453; poor Joe, 114; panic grass, 86; sedge (*Carex* spp.), 24; paspalum, 2 and wild bean (*Strophostyles leiosperma*), 2.

A *Reithrodontomys* nest built in a rose bush several feet from a quail trap was examined and found to contain 271 sorghum seeds (*Sorghum vulgare*). The mouse had removed the seeds from the baited area and carried them to the nest. Another harvest mouse nest examined December 12, 1951, contained four seeds of *Bumelia* sp. and one of goatweed.

A nest used by a white-footed mouse, located approximately four miles east of Benchley, Robertson County, contained the remains of approximately 75 goatweed seeds. In the same general area, excavated runways of *Perognathus hispidus* revealed numerous seeds of burr clover (*Medicago hispida*) and goatweed. Sixty-one goatweed seeds were removed from the cheek pouches of an adult hispid pocket mouse that was found dead during a hunting trip in Brazos County, Texas, on March 30, 1951. Glass (1946) noted that a burrow of *Perognathus hispidus* excavated near College Station, Texas, contained about one pint of *Diodia teres* seeds, while Blair (1937) found this species utilizing seeds of *Croton, Oenothera, Andropogon, Bumelia, Bouteloua, Prunus, Carex, Opuntia,* and several others.

The available data indicate that rodents, particularly *Reithrodontomys, Perognathus,* and *Peromyscus,* are probably of greater significance in competing with bobwhites in a given area where they all occur than are the various song birds. Extremes in varying climatic and habitat conditions influence locally the production of seeds and other foods. An area will differ from a neighboring one to a certain extent; hence, the carrying capacity of one will exceed or be less than that of the other. Because of the variability that exists, it becomes extremely difficult to establish conclusively one factor or another as significant in limiting quail numbers. This difficulty is especially marked when calculating food production in an area and in determining what species are and are not competing with the bobwhite for that food.

Summary

1. During 1950 and 1951 a study of the food and cover relationships of the bobwhite quail was undertaken in the Post Oak Region of East-central Texas.
2. Thickets of McCartny rose and stretchberry were utilized more often than any other type of cover by quail for escape and protection. Wood's edge afforded satisfactory cover only when stretchberry and yaupon were abundant. Pastures containing perennial grasses (little bluestem and silver beardgrass) were also valuable as cover.
3. Goatweed (*Croton* spp.) constituted one of the most important foods in the diet of bobwhites examined during this study. Acorns were a valuable source of food during the year of high mast production (1950). Data indicated that abundance and availability were the primary factors controlling the bobwhite's selection of food.
4. Overgrazed pastures containing stands of *Croton,* interspersed with species of *Lespedeza, Strophostyles, Panicum, Paspalum,* and other seed-producing herbs afforded a large percentage of the yearly food supply. Goatweed was available and was utilized throughout most of the year; species of panic grass

and green vegetation were important in early spring and insects were consumed in large numbers during the summer.

5. Stomach examination of song birds common in the Post Oak Region showed that little or no competition for available food exists between them and the bobwhite, with the possible exception of large migrant flocks of mourning doves and certain blackbirds. Seed-eating rodents (*Perognathus, Peromyscus,* and *Reithrodontomys*) exhibit a certain amount of competition with bobwhites due to their consumption of foods most valuable to the quail.
6. Food and cover cannot be considered or treated separately from the other ecological constituents of the environment. Although many other factors enter into the problem of quail management, suitable cover and sufficient food supply during the critical periods of the year are basically the most important factors in quail survival in East-central Texas.

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A REEVALUATION OF PLANT COMMUNITIES WITHIN THE PHEASANT RANGE IN THE NEBRASKA SANDHILLS

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Introduction

The writer was employed from 1935 to 1943 at the Valentine National Wildlife Refuge, located in Cherry County, Nebraska, the site of the pheasant studies reported by Sharp and McClure in McAtee (1945). Plant communities of the area, studied during the period, were reevaluated during 1950 and 1951 after a series of wet years. Striking changes had occurred in these vegetational zones since 1942. Two of the most important plant communities, namely, dry marsh and forb, had been replaced in the habitat and as a result were of minor value for pheasants. The forb communities had been replaced by grasses; the dry marshes had been flooded by water to a depth of several feet.

The pheasant population was lower during these latter years than at anytime during the drought (1935 to 1941). Requirements of optimum pheasant range in this region have been summarized by the above authors as follows: "A pheasant population in the sandhills of north-central Nebraska develops in direct ratio to the balanced habitat. The range must include marsh, meadow, weed, and shrub communities within the daily cruising radius of this upland game bird."

Ring-necked pheasants were introduced into Cherry County, Nebraska, in the decade previous to 1910. The population remained static until the early thirties when a sudden upswing occurred. The greatest concentrations by 1938 in the heart of the sandhills were along streams, about marshes, and the small cultivated areas. The fewest birds were found in areas of the sandhills that had no streams or marshes. Populations about streams and marshes averaged from 25 to 70 birds per square mile, as was the case in the vicinity of the Valentine National Wildlife Refuge in 1940. Open seasons were declared for the first time during the late thirties. The population began a decline in 1943 and continued up to 1951. Mohler (1949, 1950, and 1951) reports the pheasants seen per 100 miles by mail carriers in Cherry County, Nebraska, during April 1949, 1950, and 1951. Numbers counted averaged as follows: (1) 1949: (8), (2) 1950: (7) and (3) 1951: (7) per 100 miles. Average counts per 100 miles during July of the above years were 10, 7, and 4 respectively.

The purpose of this report is to describe some of the effects of climate on plant communities in the Nebraska sandhills over a 21-year period. The objectives are: (1) to review the precipitation records during 1931-51, (2) to relate changes in plant communities since 1935, (3) to discuss the ecological implications in the pheasant range, and (4) to indicate changes in pheasant populations.

Precipitation Changes over a Twenty-One Year Period

Following a wet period in north-central Nebraska in 1929, a drought began in 1931 and was broken with the close of 1940. This was the longest and most intense dry period since 1900 (Nicholas 1950). Precipitation during these drought years averaged 15.24 inches annually. The region, since 1941, has experienced a series of wet years. The summer of 1951 was considered a wet peak equalled or

surpassed only eight times since 1900. Thus, a third of the wet seasons have occurred since 1943. Annual precipitation from 1941 to 1951 averaged 20.25 inches.

The driest seasons for the past 51 years were recorded in 1937 with 11.13 inches of precipitation and in 1934 with only 11.52 inches. The average annual precipitation (1936 to 1938), following the hard winter of 1936, was 13.91 inches. A similar severe winter occurred in 1949 during the period of wet years that followed the drought. Precipitation during 1949 to 1951 averaged 21.45 inches annually.

Ranches in 1930 were stocked with herds in accordance with the carrying capacity of previous wet seasons. With the advent of drought, herds were not reduced. Ranchers kept cattle as a means of making a living and hoped that rains would return. The rains never came and overgrazing of the region became obvious by 1935. The continued drought brought about herd reduction. Overgrazed and trampled areas were taken over by communities of weeds. Former lakes and marshes receded drastically or dried up. The pheasant population experienced favorable conditions in this area and an irruption resulted during 1938-42.

A reduction in the numbers of cattle grazed during the latter years of the drought had no immediate effect on the effect on the luxuriance of the forbs. These plants were able to dominate formerly occupied areas due chiefly to factors influenced by drought. Meadows on the Valentine National Wildlife Refuge, for example, reserved exclusively for duck nesting cover in 1936 were unmowed and ungrazed. The accumulation of old mat forming a dense mulch of dead grasses had by 1939 developed conditions where weeds were replacing sodded areas.

Many species of grasses failed to flower and produce seed during the drought years. Seedlings were unable to become established on the dry soil. Annual weeds competed for the available moisture and were able to hold the grasses in check. Years of high precipitation favored the grasses which were able to dominate the communities. The carrying capacity for cattle had been more than doubled in 1951 for the same areas grazed in 1938. Grasses have thrived as a result of the increased moisure. Present increased grazing has benefited the luxuriant growth of grasses by reducing their density and by eliminating the accumulation of dead culms, "old mat," or mulch which is characteristic of ungrazed areas in this tall grass region. A study of an undisturbed grassland by Weaver and Rowland (1952) revealed that a considerable reduction in yields resulted from excessive mulch.

A Comparative Rating of Pheasant Range Communities

Pheasant range communities, at the close of 1941, are described by Sharp and McClure in McAtee (1945: 207-209). Plant species supplying the major foods of the ring-necked pheasant are listed on p. 210 of the above report. Communities producing these food plants have declined due to successional changes in the composition of the vegetation. Conditions existing in these habitats in 1950 and 1951 are summarized in the order given in the previous published report.

Springy marshes

1. The return of surface water to marsh areas, which were dry or nearly so, during the late summer, fall, and winter months of 1936-40 has eliminated the pheasant from this community. These areas, since 1944, have been covered with water three to five feet deep throughout the year. These former pheasant habitats are now true aquatic communities producing muskrats and fish. The valuable winter cover and food formerly utilized by pheasants no longer exist. Former important food plants in the diet of this game bird, namely, jewelweed (*Impatiens capensis*), nodding smartweed (*Poly-*

gonum lapathifolium L.), beggar ticks (*Bidens cernua* L.), and duck potato tubers (*Sagittaria latifolia* Willd.) are not available. These species made up ten per cent of the pheasant's fall, winter, and spring foods during the dry years. Cover value of this community for pheasants was also of inestimable value. Thickets of willows have been partially inundated and in many cases have died out. Other coarse plants such as *Phragmites* and *Scirpus* have deteriorated in value in winter shelter.

Meadow communities

2. This habitat has been divided into three zones, namely, the wet meadow, medium-moist meadow, and true prairie. With increased precipitation, the wet meadow species of grasses (*Spartina pectinata* Link.), for example, have invaded the former moist meadow zone. This upper invasion of wet meadow species, due to high water tables, has greatly reduced forbs such as ragweed, dandelions, and sour dock. These formerly occupied sparsely grassed areas. Bluegrass has also been crowded considerably by the taller coarser grasses.

The true prairie zone deteriorated rapidly during the early years of the drought. Areas denuded of grasses were commonly interspersed throughout this type. Weeds invaded and formed dense colonies. Knotweed (*Polygonum ramosissimum* Michx.), western ragweed (*Ambrosia coronopifolia* T. & G.), sunflowers, Ellisia (*Ellisia nyctelea* L.), and trefoil (*Acmispon americanus*) were characteristic species. A forb-grass zone resulted. The increased density of grasses in the true prairie zone, since 1943, has reduced weeds formerly valuable as foods for pheasants. Western wheatgrass (*Agropyron smithii* Rydb.), switchgrass (*Panicum virgatum* L.), and Canada wild-rye (*Elymus canadensis* L.) have become dominant.

Sand dune community

3. The sand dune community, including the sandhills proper, comprises about 63 percent of the acreage included in this study. The early years of the drought through 1934, with its hot winds, accompanied by heavy grazing and trampling, caused considerable deterioration especially along the bases of the slopes. Six-week fescue (*Festuca octoflora* Walt.) invaded early to blanket the exposed soil. This low, shallow-rooted, early maturing grass was rapidly replaced by weeds. Sandhill sunflower (*Helianthus petiolaris* Nutt). was one of these valuable forbs. Weeds were dominant on these sites by 1937. This community contributed substantially to the food of pheasants chiefly in the form of dry and fleshy fruits.

The density of grasses based upon an analysis of permanent, circular 100 square foot plots had increased as a result of the abundant moisture since 1942. Weedy plants that were able to flourish during the drought years have since been unable to compete with the grasses. Sandhill sunflowers, Russian thistle (*Salsola pestifer* A. Nels.), tumbleweeds (*Cycloloma atriplicifolium* [Spreng.] Coult.) puccoon (*Lithospermum gmelinii ETAI* Hitchc.), and other dry-fruit-producing forbs contributing to the pheasant's livelihood have been reduced in density or have been eliminated. Those surviving have been suppressed as a result of competition from native grasses and do not produce fruit as abundantly as in former years of drought.

Upland shrub community

These communities, comprising about two per cent of the acreage, have remained unchanged or have been favored by the increased seasonal moisture. Chokecherry (*Prunus demissa* [Nutt.] D. Dietr.) and wolf- or coralberry (*Symphorocarpus occidentalis* Hook.) were the principal shrubs in this type of cover.

Weed or forb community

5. Several forb areas, adjacent to meadows and marshes, included in our earlier studies were inspected during 1950 and 1951. These communities dominated plots of 50 to 200 acres in area. Native grasses formerly on these sites in 1930 were damaged by the intense drought and heavy trampling by livestock on winter feed plots. Forbs were dominant on these sites when first observed in 1935. Pheasant winter populations centered around such habitats during 1936-42. One observing these grass covered sites in 1951 for the first time would scarcely believe they had been "weed patches" ten years previously. Pheasants collected from these sites during the fall, winter, and spring months of 1937-39 revealed that their crops were filled with food, the bulk of which was derived from weeds.

This portion of the pheasants' feeding range was eliminated or drastically reduced during the wet years following 1941. Many sites that supported pure stands of weeds during 1935-1942 are now occupied by native grasses, while forbs in others are only sparsely represented by the present grass community. Forbs producing the bulk of staple dry fruits, found in the diet of the pheasants, have undergone greater decreases in abundance than those that do not contribute to the welfare of this game bird. The former species of forbs are characteristic invaders representing the pioneer stage of seral development; the latter are more permanent and are able to exist in the grass-dominated communities.

Could the over-population of pheasants have contributed to the decrease in the more important annual weed species by gleaning all available fruits? The decline of the important weed species was uniform over the sandhill region. Areas that had never supported a pheasant population revealed a similar dearth of forbs comparable to that found on areas of high populations.

Pheasants gleaned a substantial portion of their fall, winter, and spring food supply from the forb community during the dry years. A restudy of permanent check areas revealed that plants of knotweed have become dwarfed or slender in form and reduced by 90 per cent of its former abundance. The Russian thistle has been eliminated. This plant appears to have been replaced by the Mexican fireweed (*Kochia scoparia* Schrad.) which is of little value as a source of food for this upland game bird. Other important pheasant food plants such as lambsquarters (*Chenopodium leptophyllum* (Moq.) Nutt.), pigweed (*Amaranthus retroflexus* L.), common ragweed (*Ambrosia elatior* L.), western ragweed, Ellisia, beeplant (*Cleome serrulata* Pursh), wild bean (*Strophostyles leiosperma* T. & G.) Piper), and trefoil have been crowded out on some former sites or have been greatly suppressed on others by the succession of native grasses. Although sandhill sunflower has persisted, competition from grasses has suppressed its former size and density. Two areas with permanent plots checked in 1951 revealed that its density had been reduced from 90 to 10 per cent of ground coverage. Horse weed (*Iva xanthifolia* Nutt.) has persisted but its distribution and abundance are not sufficient to compensate for any of the food supply lost by the disappearance of other valuable food-producing weeds. The forb community had been practically eliminated as a valuable source of pheasant food by 1950.

Increased rainfall following 1941 began bringing about a gradual change in the plant communities. This change had not made sufficient progress to affect the population in 1942. Time was required to restore water tables to normal levels but by 1944 dry marshes and lakes had filled with water to a depth of 3 to 5 feet. Native grasses favored by the increased moisture began invading forb communities and by 1951 had become dominant. The pheasant population was faced with a changing habitat which was

growing progressively more unfavorable. It was during the wet period that the population descended sharply and has since continued to decline.

Discussion of the Ecological Implications in the Pheasant Range

The Russian thistle may be considered the key species indicator of an optimum pheasant habitat in the Nebraska sandhills. When favorable environmental conditions return, as was the case during the drought years, wildlife managers will know by the abundance of this species that other conditions in the habitat are also probably favorable for this game bird. Dry marshes as well as other valuable communities will then be present within the daily feeding range. The ringneck pheasant is not adapted to grass-dominated communities. Former food habits studies conducted in these areas show that coarser native grasses contribute little in maintaining a year-around food supply. The pheasant thrives best in or adjacent to agricultural lands; however, in non-agricultural areas a good population may exist where weedy communities and winter cover are abundant. Cover afforded by dry marshes appears indispensible in the winter needs of this game bird in the Nebraska area under study. Observations in South Dakota indicate that similar areas were also of great value in favoring the 1935-42 populations.

The Nebraska sandhills are not ideal pheasant range due to the absence of agriculture. The drought years apparently created conditions favorable for this game bird. With the advent of successive wet years plant succession has erased these favorable conditions. The composition of plant communities in the sandhills has changed strikingly over the past ten years—so much so that the pheasant can no longer survive in its former abundance. The sandhills is regarded as an area on the outer limits of the range of pheasants. The writer believes that, in this area, pheasant populations are regulated chiefly by changes in plant communities brought about by periods of drought or abundant rainfall. Annual winter temperatures are not believed to be a controlling factor when optimum food and cover conditions exist.

Conclusions on Pheasant Populations

The hard winter of 1949 was considered by some as a factor responsible for the present dearth of pheasants in the Nebraska sandhills. The population was on a decline by 1945 and finally suffered a severe drop during the winter of 1948-49. The fall population in 1951, two years following the severe winter, indicated no recovery. Those birds remaining since 1949 were faced with the counter-force of an unfavorable habitat. Summer foods were adequate on the area but a dearth of winter food and shelter was obvious.

The winter of 1935-36 was equally severe. Deep snow covered food supplies and continued sub-zero weather took a heavy toll of birds. However, favorable seasons that followed, with dry summers and an abundance of food and cover, were conducive to a rapid recovery. The population by 1938 was nearing a peak.

The continued decline in pheasant populations following the severe winter of 1948-49 may be accounted for, in part at least, by the present food and cover conditions as contrasted with those existing after the winter of 1935-36. Predation was never of importance during years of a high population. There is no reason to believe that it has been of significance as a controlling factor during recent years. The loss of valuable winter cover and food would naturally subject the population to predation which would not occur in optimum habitats.

There has been a general drop in pheasant populations in the Great Plains region during the period of the decline in the sandhills of Nebraska. Conditions contributing may not be identical in all cases to those given in this report. It

was noted, however, while on a tour of Todd County, South Dakota in September, 1951, that the Mexican fireweed had replaced the Russian thistle as was the case in the Nebraska sandhills. The trend was to almost pure grasslands. Former extensive forb areas have been or are rapidly being replaced by native grasses. This change in pheasant habitat since the depression and drought years has reached into many states.

Plant successions in the Nebraska Sandhills and South Dakota, land-use trends including use of modern farm machinery, increased crop production, new developments in harvesting methods, and intensified clean farming in others have played their role in reducing the numbers of this bird. Leedy and Dustman (1947) reported that approximately two-thirds of the pheasants nested in hay meadows in Ohio during the years 1939-1941. These areas representing a cross-section of the pheasant range in that state had been reduced to almost one-fourth by 1946 due to an increase in agricultural crops. Pheasant nesting cover consequently was considerably reduced since fields of corn, soybeans, etc., were not suitable for nest site locations. The development of hay harvesting methods, reported by the above investigators and Wight (1950) in Pennsylvania, have had a detrimental effect on pheasant nests and the incubating bird. Clean farming such as stubble clipping, late mowing of weed crops, the elimination of fence rows, etc., have reduced fall and winter cover. The change from corn crops to grasslands in Todd County, South Dakota, is another case where the weed and corn crop formerly producing winter food and cover has been replaced by forage crops of little winter food and cover value.

Summary

1. The drought years 1930-40 were the most continual and intense since 1900. Precipitation averaged 15.24 inches annually during this period as contrasted to 20.25 inches during 1941-52, a series of wet years.
2. Grasslands communities deteriorated rapidly during the early years of the drought. The denuded spaces were rapidly revegetated by forbs. Lakes and marshes receded drastically or dried-up. The resulting habitat was optimum for pheasant populations.
3. Wet years following 1941 have favored the return of native grasses. Former dry marshlands have been inundated and weed species producing the bulk of the pheasant food have declined or disappeared.
4. Two severe winters occurred during the 21-year period. Pheasant populations responded quickly following the hard winter of 1935-36, but failed to increase during the two years following the rigorous weather of 1948-49. The habitat, during the latter years, had deteriorated while, following 1936, it was favorable for pheasants.
5. There has been a general decline in pheasant populations in the Great Plains since 1942. The area has reverted to grasslands on the uplands with depressions filled with water. The author's observations on plant successions in this region since 1935 have revealed a gradual loss of pheasant winter food and cover.

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COMPARATIVE EFFECT OF SEED TREATMENTS UPON SEEDLING EMERGENCE IN SEVEN BROWSE SPECIES

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INTRODUCTION

Artificial propagation by seed of palatable native browse species may be an economical way of improving big game forage and watershed values. Success of artificial reseeding generally requires that the planted seeds germinate soon after growing conditions become favorable. On the other hand, under natural conditions, persistent and variable seed dormancy may often be a factor favoring survival of a species. Such dormancy is in no way uncommon among native browse and tree species. This adaptation, however well-geared to the timeless regime of nature, presents an obstacle to efficient artificial seeding of these refractory native species. It can be overcome only by learning the processes for unlocking the seed dormancy perculiar to each species. This paper presents effects of comparable seed treatments upon seedling emergence of seven browse species potentially important in the improvement of big game ranges and control of erosion throughout much of the northwest mountain region.

Results from the tests show the extreme importance of proper seed treatment of these browse species if germination is to be hastened, and what some of the effective treatments are for each species. Most of the data support results from other studies, thus strengthening the base for generalizations. In a few instances, contradictions point up the need for more investigations.

COLLECTION AND PREPARATION OF SEEDS

Seeds of the seven browse species—redosier dogwood, *Cornus stolonifera* Michx.; antelope bitterbrush, *Purshia tridentata* (Pursh) DC.; redstem ceanothus, *Ceanothus sanguineus* Pursh; snowbrush ceanothus, *C. velutinus* Dougl.; Saskatoon serviceberry, *Amelanchier alnifolia* Nutt.; western chokecherry, *Prunus demissa* (Nutt.) Walp.; and Rocky Mountain maple, *Acer glabrum* Torr.—used in this study were collected in Lincoln County in northwestern Montana by Jack Schmautz and Ade Zajanc, formerly of the Montana State Fish and Game Department. Bitterbrush seeds were collected in July, the others in the second half of August. Characteristics of the collection sites are summarized in Table I. Chokecherry and serviceberry seeds were depulped by hand, using water and screens. All seeds were stored in an unheated shed for about three months and then at room temperature for one and one-half months. Before testing each seed was inspected carefully and those which showed abnormalities or defects were discarded. Seeds of each of these species are known to be subject to one or more types of dormancy. Also, germination in all is epigeous, cotyledons being brought above the ground.

The number of apparently sound seed was upward to 90 per cent for all species except those of redstem and snowbrush ceanothus which were less than 50 per cent sound. All light-colored redstem and snowbrush seeds were hollow, and many of those with normal color were found to be hollow when subjected to moderate finger pressure. Worm holes in still others made rejection necessary. Even after rigid inspection many unsound seeds remained. For example, dissection of fifty apparently sound redstem seeds

TABLE I. *Characteristics of seed collection areas*

Species collected	Place	Exposure	Soil	Other characteristic species	Elevation (feet)
Redosier dogwood	Libby Creek Paul Bunyan's Grave	Level	Alluvial gravel (flood plain)	*Picea engelmanni* *Thuja plicata* *Populus trichocarpa*	2,500
Rocky Mountain maple	do.	do.	do.—except slightly higher and more fertile soil	do.	2,500
Antelope bitterbrush	Horse Range	South	Gravelly silt	*Pinus ponderosa* *Agropyron spicatum*	2,400
Redstem ceanothus	Swede Gulch	do.	Rock-silt	*Pseudotsuga taxifolia* *Pinus ponderosa*	4,000
Snowbrush ceanothus	do.	do.	do.	do.	4,000
Saskatoon serviceberry	Granite Creek	Level	Gravelly loam (flood plain)	*Alnus tenuifolia* *Populus tremuloides* *Populus trichocarpa*	2,500-3,000
Western chokecherry	do.	do.	do.	do.	2,500-3,000

showed 60 per cent well-filled, 22 per cent wormy, and 18 per cent entirely hollow or with poorly developed embryos or other defects. Attempts to separate defective from sound seeds by a water flotation process failed. Defective as well as sound seed usually sank. Because of the inevitable presence of unsound seed, emergence percentages were conservative compared to those expected from wholly sound seed.

TREATMENT OF SEEDS AND TEST CONDITIONS

Five seed treatments were tested (Table II). Three were applied to all species, while Rocky Mountain maple and western chokecherry seeds were not scarified.

TABLE II. *Seed treatments used in this study*

Treatments	Species	Duration of treatment
Exposed to winter conditions only	Redosier dogwood Antelope bitterbrush Redstem ceanothus Snowbrush ceanothus Saskatoon serviceberry Western chokecherry Rocky Mountain maple	87 days
Scarified and exposed to winter conditions	All except western chokecherry and Rocky Mountain maple	87 days
Stratified only	All species	90 days
Scarified and stratified	All except western chokecherry and Rocky Mountain maple	90 days
Submerged in hot water and stratified	All species	30 minutes 90 days

Except for redstem and snowbrush ceanothus seeds, which were carefully punctured with a dissecting needle, all seeds were scarified by rubbing them individually over fine sandpaper until the seed coat was worn through. (All seed coat abrading or puncturing, however, will henceforth be referred to as "scarification.") After scarification, the seeds were covered and stored in a refrigerator for three to seven days to keep drying at a minimum before either being stratified or prepared for outdoor exposure. For the hot water treatment, 90 c.c. of boiling water were poured over each lot of 100 seeds in a 100 c.c. beaker and al-

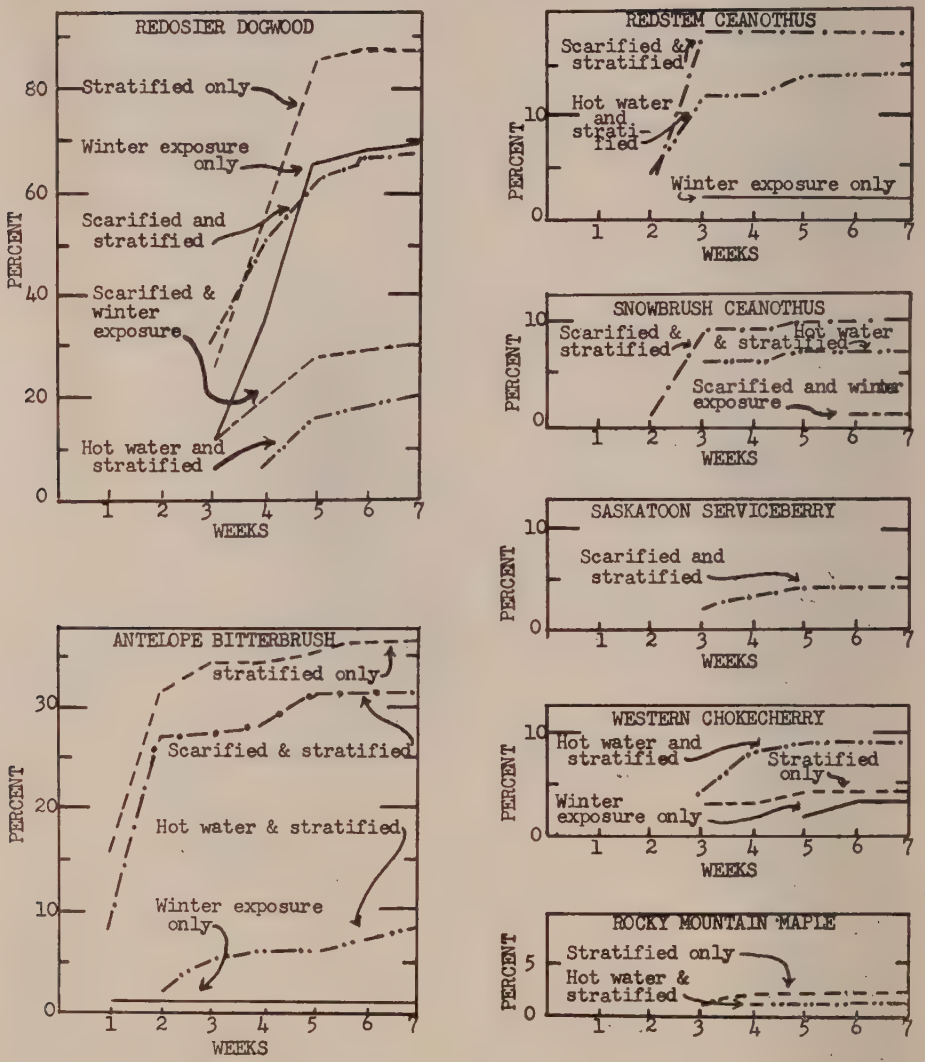

FIG. 1. Accumulative seedling emergence for seven browse species relative to treatment of seed. Only those treatments under which emergence occurred are shown for each species.

lowed to cool at room temperature for 30 minutes.

Seeds exposed to winter conditions were planted in well-watered soil flats and set outside on the ground on January 2. Because little snow fell the soil became dry, hard, and cracked before the flats were brought in for germination on April 2. Mean monthly temperatures were about 22°, 28°, and 37° F. for January, February, and March, respectively (U. S. Weather Bureau 1951).

Stratification was accomplished by placing the separate seed lots in sausage casings containing moist, sterilized, fine sand, packed in moist peat, and stored at about 35° F.

Seeds were planted in greenhouse flats containing loam soil previously mixed for uniformity. One hundred seeds of each

species were used for each treatment. These 100-seed lots were divided into sublots of 25 seeds each to provide replication. Sublots were planted in individual rows, ¾-inch deep, between April 3 and 5, except those planted on January 2 for winter exposure.

All flats were placed side by side in the greenhouse and watered almost every day to keep the soil moist. Seedlings were counted the same day each week for seven consecutive weeks. These counts served as the primary criterion for appraising treatment effect on seed germination.

Daily greenhouse temperatures usually ranged between 45° and 80° F., with an average maximum of 79° and minimum of 45° for April, and 83° and 47°, respectively, for May.

At the end of the test period as many ungerminated seeds as possible of each species were recovered from two rows of each treatment by a washing-screening process. The recovered seeds were dissected and classified as to apparent soundness.

Results

Comparison of species

Antelope bitterbrush emerged first after planting (Figure 1). Thirty-two per cent of the final total came up during the first week and 80 per cent by the end of the second week. This rapid emergence was no surprise, as many of the seeds which had been stratified only and those scarified and stratified had already started to germinate when planted. Redstem and snowbrush seedlings began to show by the end of the second week, and over 80 per cent of the final total were up by the end of the third week. Seedlings of other species did not appear until the third week. By the end of the fifth week emergence was at least 95 per cent complete for all species.

In general, the treatments which produced the highest per cent germination also showed earlier emergence of the first seedlings than treatments producing a lower total germination. For example, in the case of antelope bitterbrush and redosier dogwood, the hot water treatment followed by stratification did not promote emergence. Likewise, the first seedlings from this treatment emerged a week later than those from more effective treatments. Seeds exposed to winter conditions also tended to germinate somewhat later than the others. Such delay would have obvious disadvantages in field plantings, where rapid response to favorable conditions is usually desirable.

Redosier dogwood gave the highest per cent of seedling emergence irrespective of treatment. Antelope bitterbrush was second, and Saskatoon serviceberry and Rocky Mountain maple responded least (Table III). Part of the relatively high emergence of redosier dogwood may be attributed to the presence of two viable embryos in many of the double-celled fruits. Practically no germination of redstem and snowbrush occurred except in the hot water and scarification treatments involving an increase in seed coat permeability plus after-ripening through stratification.

Combining the total per cent emerged seedlings with the per cent of sound seed remaining at the end of the trial shows the potential germination—or the percentage which might eventually be expected to produce seedlings (Table III). By comparing potential germination with emergence one may glean additional insight into the effect of the hastening treatment. For example, although scarification plus stratification produced the highest emergence in both ceanothus species, this treatment, by increasing seed spoilage, gave a potential germination, ranking fourth among the five treatments. In contrast, seeds of these species exposed only to winter conditions produced practically no seedlings but retained a higher potential germination than ceanothus seeds treated differently. This information is of particular value in plantings

TABLE III. *Seedling emergence and potential germination* of seed of seven browse species subjected to various treatments*

Seed treatment	Redosier dogwood		Antelope bitterbrush		Redstem ceanothus		Snowbrush ceanothus		Saskatoon serviceberry		Western chokecherry		Rocky Mountain maple	
	Per cent emergence	Potential germination	Per cent emergence	Potential germination	Per cent emergence	Potential germination	Per cent emergence	Potential germination	Per cent emergence	Potential germination	Per cent emergence	Potential germination	Per cent emergence	Potential germination
Exposed to winter conditions only	69	83	1	1	2	66	0	88	0	16	3	87	0	72
Scarified and exposed to winter conditions	30	44	0	0	0	0	1	1	0	2	†		†	
Stratified only	87	97	36	54	0	38	0	54	0	78	4	92	2	62
Scarified and stratified	67	73	31	35	18	18	10	16	4	38	†		†	
Hot water and stratified	20	62	8	32	14	52	7	41	0	72	9	87	1	75

*Potential germination is the sum of the percent of emergence and per cent of sound seeds remaining at the end of the test. Figures given are conservative, because not all seeds were recovered in each case.

†Not given these treatments.

where prompt germination is not necessarily desired.

The potential germination was deleteriously affected by scarification plus winter exposure in all species so treated (Table IV). Even winter exposure alone was adverse for antelope bitterbrush and Saskatoon serviceberry. Stratification alone gave the highest potential germination for most species but was ineffective in hastening germination in some cases.

Unlike the mechanical breaking of the seed coat by scarification, which undoubtedly facilitated the entrance of organisms and drying of the winter-exposed seeds, the hot water treatment did not cause increased spoilage of seed (Table IV). Therefore, lots treated in that way usually maintained a high potential germination.

Redosier dogwood

With redosier dogwood, stratification alone gave emergence which averaged 18 per cent higher than the next best treatment. This treatment also gave the best potential germination. Winter exposure alone gave excellent response, but in comparison, scarification of seeds subjected to winter conditions and the hot water treatment plus stratification greatly reduced emergence of seedlings. Potential germination was substantially lower for the seeds scarified and subjected to winter exposure than for those which received the other treatments. The low percentage of sound seeds from the other treatments can probably be accounted for by the high germination which would automatically tend to leave a higher proportion of unsound seeds among those which had not germinated. In some cases, the stone of the seed had partially split open without resulting in germination.

Antelope bitterbrush

Stratification without other treatment also gave highest emergence and potential germination in antelope bitterbrush while exposure to winter conditions was poorest. Scarification plus stratification resulted in only slightly lower emergence, but a substantially lower potential germination, than stratification alone. The hot water plus stratification treatment positively inhibited germination, ap-

TABLE IV. *Total number and per cent of sound ungerminated seeds* recovered at close of test*

Seed treatment	Redosier dogwood		Antelope bitterbrush		Redstem ceanothus		Snowbrush ceanothus		Saskatoon service-berry		Western choke-cherry		Rocky Mountain maple	
	Number recovered	Per cent sound	Number recovered	Per cent sound	Number recovered	Per cent sound	Number recovered	Per cent sound	Number recovered	Per cent sound	Number recovered	Per cent sound	Number recovered	Per cent sound
Exposed to winter conditions only	21	33.3	21	0	34	94.1	45	97.8	28	28.6	47	89.4	47	89.4
Scarified and exposed to winter conditions	31	22.6	47	0	5	0	3	0	12	18.3	†		†	
Stratified only	22	22.7	25	36.0	19	100.0	36	75.0	40	97.5	42	71.4	45	97.8
Scarified and stratified	25	12.0	42	4.8	11	0	13	23.1	42	40.5	†		†	
Hot water and stratified	30	70.0	42	28.6	24	79.2	24	70.8	41	87.8	43	86.0	40	97.5

*Based on seeds recovered from two rows, each of which originally had 25 seeds for each species-treatment combination, except for antelope bitterbrush exposed to winter conditions where seeds were recovered from only one row.
†Not given these treatments.

parently due to the hot water part of the treatment, and the 200 seeds exposed to winter conditions failed to produce more than one seedling.

Both winter treatments resulted in complete spoilage of ungerminated seeds. In contrast, hot water plus stratification and stratification alone left 29 and 36 per cent sound seeds, respectively, despite comparatively high emergence. Seventy-four per cent of the emerged seedlings "damped-off" by the end of the test. A moderate number died before emergence under all treatments, probably due to the same cause. It seems likely, too, that because some of the seeds germinated while still stratified they may have been injured in planting. This early sprouting points to the importance of keeping the stratification period to less than three months. Two to three months of stratification have been recommended (U. S. Forest Service 1948).

Redstem and snowbrush ceanothus

Response of redstem and snowbrush differed slightly in magnitude but was similar otherwise. Scarification plus stratification was the most effective hastening treatment, with hot water plus stratification a close second. Curtis (1952), however, reported much higher germination of snowbrush seeds soaked in hot water previous to stratifying than for those abraded by shaking violently with small stones. Based on the experience of the author, this was likely due to the resistance of these seeds to either wear or breakage, which makes scarification difficult. Comparatively, however, the hot water treatment resulted in little seed deterioration (Table IV) or decrease in potential germination (Table III). Low emergence even where the seed coat was punctured suggests that an increase in stratification beyond three months might be desirable. Ready germination of seeds of these species following a fire, after two or more years of dormancy, also indicates that stratification may be prolonged without injury.[1]

While winter exposure alone did not hasten germination, neither did it, nor the other treatments in which the seed coat was not broken, lower potential germination. Furthermore, exposure to

[1] Jack Schmautz. 1951. Personal communication.

winter conditions alone left the recovered seeds glossy, although lighter brown, than before planting, while about 50 per cent of those stratified were very dull, suggesting that stratification aids in seed coat deterioration as well as in after-ripening.

Rocky Mountain maple

Only three seedlings emerged from the 300 Rocky Mountain maple seeds tested. Although a high proportion of the recovered seeds had embryos which were obviously alive and green, they were shrivelled and failed to show growth when placed in moist gauze for one week. No published information was found to explain the poor response of this species. A fall planting, however, in Lincoln County gave a germination the following spring of 20.4 per cent (Schmautz and Zajanc 1950). This suggests that a longer stratification period might help to break dormancy.

Comparative seedling vigor

Survival of seedlings depends greatly on their vigor and resistance to disease. Even though the experiment was not designed to test this point, it may be significant that the percentage of seedlings lost from damping-off ranged from 12.5 and 25 for western chokecherry and redosier dogwood, respectively, to 75 for antelope bitterbrush and Saskatoon serviceberry. From the standpoint of overall robustness of seedlings surviving at the end of the trial, chokecherry was easily first, dogwood second, bitterbrush third, with maple and the others following. Redstem seedlings in this trial were more robust than those of snowbrush.

Discussion

In evaluating the response of these seeds to various treatments in relation to possible field practice, these facts should be kept in mind: 1. the stratification period (90 days) given western chokecherry and Saskatoon serviceberry was definitely not as long as recommended by the most comprehensive modern authority (U. S. Forest Service 1948); Rocky Mountain maple also may require a longer stratification period, although apparently little is known of its requirements; 2. outdoor exposure was for a shorter period than would be the case if the seed were planted in the fall; and 3. outdoor temperatures and moisture conditions in the flats subjected to winter conditions were too low much of the time for maximum after-ripening of the seeds.

Contrasting results from these tests with those secured by Schmautz and Zajanc (1950) in a fall field planting in Lincoln County throws additional light on the requirements of these species. They planted untreated seeds in September about one-half inch deep.[2] Abundant rains in October and heavy snowfall which came early enough to keep the ground from freezing provided the moist, cool conditions necessary for good after-ripening over a period of five or six months.

The following spring emergence for Saskatoon serviceberry, western chokecherry, and Rocky Mountain maple was 29, 38, and 20 per cent, respectively. This was about 7, 4, and 10 times as high emergence as obtained with the most successful treatment of these species reported herein. The obvious explanation is that the long after-ripening in the field test was much more conducive to germination of these species than the three-month stratification period used in this study.

The field planting of redosier dogwood, antelope bitterbrush, and snowbrush by Schmautz and Zajanc gave only 11, 18, and 0.12 per cent emergence, respectively. In contrast, emergence of these species under the most favorable treatments used in this study was 8, 2, and 83 times as good, respectively. The difference in response of antelope bitterbrush and redosier dogwood in the field as compared

[2] Jack Schmautz. 1951. Personal communication.

to the results reported in this paper was again likely a function of the length of the stratification period. With these species, however, the best after-ripening period was nearer three months than the five or six which appeared to favor the serviceberry, chokecherry, and maple seeds. The long after-ripening period in the fall field planting may have broken the dormancy of the dogwood and bitterbrush seeds before growing conditions were favorable and resulted in the death of many of the seed embryos or small seedlings.

The extremely low germination of snowbrush which Schmautz and Zajanc observed is further verification of its need for seed coat treatment. Curtis (1952) also got practically no germination of stratified snowbrush seeds which had not been treated to improve permeability of their seed coats.

It is clear that fall planting, without seed treatment may or may not provide the conditions necessary for proper after-ripening of these browse seeds. The specific microclimate currently prevailing, relative to the requirements of a given species, would largely dictate the per cent of emergence. Therefore, controlled treatment in accordance with the requirements of the individual species followed by spring planting would likely provide higher success than would fall planting of untreated seeds.

Summary

Seeds of seven shrubby species, collected in northwestern Montana, were treated in various ways and placed under greenhouse conditions to ascertain the relative effect of the treatments upon seedling emergence. Species used were redosier dogwood, antelope bitterbrush, redstem ceanothus, snowbrush ceanothus, Saskatoon serviceberry, western chokecherry, and Rocky Mountain maple. Seeds of all species were exposed to winter conditions in greenhouse flats, stratified, or submerged in hot water before stratifying. In addition, all except western chokecherry and Rocky Mountain maple were scarified and exposed to winter conditions or scarified before stratifying. In each case, exposure to winter conditions and stratifying were for about three months.

Antelope bitterbrush and redosier dogwood responded best to stratification only. Dogwood produced by far the largest number of seedlings and some seed germinated under all treatments. It was the only species which responded favorably to winter exposure.

Response of redstem and snowbrush ceanothus to the treatments was similar in kind but not in magnitude. Scarification of seed coat and stratification combined gave best results.

Apparent resistance to damping-off was high in dogwood and chokecherry seedlings, low in serviceberry and bitterbrush, and intermediate in the others. Scarification, especially of seeds exposed to winter conditions, increased seed spoilage during the germination period.

It is suggested that controlled treatment of seed followed by spring planting will likely give higher success than fall planting of untreated seeds.

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NUTRIENT CONTENT OF LEAF LITTER OF TREES IN THE NORTHERN ROCKY MOUNTAINS

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Introduction

Considerable interest has been directed to the study of the chemical composition of tree leaves. It was discovered long ago that species differ in their abilities to extract nutrients from the same kind of soil, and that the minerals are not similarily disposed in the tissues, with a result that their litter varies considerably in composition. The silviculturist sometimes finds it desirable to maintain in a mixed stand certain trees that produce low-value wood, only because they are useful in maintaining soil fertility for associated valuable species. The speed of rehabilitation of waste-lands and eroded areas varies with the species used in reforestation. Game management must often take into account the nutrient content of foliage available for browsing. Some analyses have been made in the hope that a reliable method of evaluating soil fertility could be discovered. Although nutrient content often appears unrelated to soil fertility as indicated by chemical analyses of soil or by vigor of growth, special correlations of local significance have found with sufficient frequency that this relationship always deserves study. In any inquiry into why trees grow where they do, the varied influences of the different species must be given careful consideration, for small initial differences in environment may cause differences in the pioneer vegetation, then the contrasted floras add so much more difference as to obscure the primary factor that caused initial divergence (Chandler 1939).

Despite the importance attached to the subject, only indirect information was available for just one species of the tree flora of the northern Rocky Mountains, when the present study was undertaken. In summarizing North American literature on the chemical composition of litter of about 60 trees that have been analyzed, Kittredge (1948) listed *Populus tremuloides,* studied in other parts of the continent, as being low in N (in the group with 0.4-0.8%), medium in P (0.15-0.3%), medium in K (0.3-0.6%), and medium in Ca (1.5-3.0%). Tarrant, *et al.* 1951 have recently published analyses of fresh leaves and of weathered litter for ten trees along the Pacific coast, four or five of which are taxonomically identical with trees included in this report. Since the chemical composition of foliage varies progressively throughout the summer, and their report does not indicate the time of year when the foliage collections were made, their data cannot be compared with the present study.

Although the primary objective of this study has been to evaluate species influences upon soil through the character of the litter they produce, several subsidiary problems were recognized. With the fundamental forest associations of eastern Washington and northern Idaho defined (Daubenmire 1952), material could be collected according to habitat types and thus make a preliminary exploration of the possibility that chemical composition may be related to variations in forest undergrowth (the Finnish "forest site types") and rate of tree growth (the North American "site index"). Also, the phytosociologic study showed two major discontinuities in forest undergrowth. A rich xerophytic undergrowth in the lower forest zones

gives way rather abruptly to a rich mesophytic flora (the *Pachistima* union) of mid-slopes. On approaching the summits of high mountains, the *Pachistima* union in turn is replaced by an extremely impoverished undergrowth (*Xerophyllum* and *Menziesia* unions). Analyses of litter from the dominant trees might make a material contribution toward an ultimate explanation of these two major phytosociologic boundaries.

Methods

In collecting litter, the aim was to obtain samples most representative of material in the condition when it first reaches the ground. Although there are no definite records available, silviculturists in the area consider autumn the principal period of abscission, hence all collections were made in September or October, except for Larix, which drops its needles in November. Trees in the vicinity of dusty roads were avoided, as were those not in good vigor.

Large cloths were spread under trees of reproductive age and the branches agitated sufficiently to dislodge dead leaves which had not fallen to the ground. All material other than discolored leaves (*e.g.,* green leaves, bits of resin, bark, twigs, cones, lichens, insects, etc.) was carefully sorted out and discarded, and approximately equal quantities of the remaining material from four or more trees were composited to make a sample considered as representative of the species on the habitat. The samples were air-dried and stored for only a short time.

Habitats were recorded according to their climax associations, as indicated by the successional trend evident in the age-class distribution among trees now on the habitat, and the character of the herbaceous and shrubby vegetation. The names of these associations, given in complete form below, are also used in naming the habitat types they characterize.

Pinus ponderosa/Purshia tridentata
Pinus ponderosa/Agropyron spicatum
Pinus ponderosa/Symphoricarpos rivularis
Pinus ponderosa/Physocarpus malvaceus
Pseudotsuga taxifolia/Physocarpus malvaceus
Abies grandis/Pachistima myrsinites
Thuja plicata/Pachistima myrsinites
Thuja plicata-Tsuga heterophylla/Pachistima myrsinites
Picea engelmanni-Abies lasiocarpa/Pachistima myrsinites
Picea engelmanni-Abies lasiocarpa/Xerophyllum tenax
Picea engelmanni-Abies lasiocarpa/Menziesia ferruginea

For detailed descriptions of these associations and general characterizations of the habitat types they indicate, see Daubenmire 1952. Nomenclature of species also follows that paper.

Most trees occur on several habitat types, and in listing the latter, the order is one of increasing moisture and/or decreasing heat. The rugged topography provides a mosaic of habitats, and upon advancing from lower timberline into the mountains relatively warm and dry habitats drop out of the mosaic while cool and moist habitats begin to appear. Thus, the altitudinal sequence implied by the order of listing is not one that can be expressed either in terms of horizontal belts or in terms of elevation above sea level, for a *Picea-Abies/Pachistima* habitat may be encountered in a cool, moist, frost-hollow at lower actual elevation than a *Pinus/Symphoricarpos* habitat near the summit of a warm, dry, south-facing slope.

Except for *Populus tremuloides,* which occurs throughout the series of forest zones, the order of listing of the trees in the tables is the most usual order in which they are encountered in going from lower timberline to highest mountains. In all, 12 species, 11 habitat types, and 45

TABLE I. *Total nitrogen as percentage of oven-dry weight of freshly fallen foliage. Samples representing the Pinus/Purshia habitat type were obtained at two locations: near the towns of Keller and Miles, Washington*

Habitat types	Species											
	Pinus ponderosa	*Populus tremuloides*	*Pseudotsuga* tax. var. *glauca*	*Larix occidentalis*	*Pinus contorta* var. *latifolia*	*Abies grandis*	*Pinus monticola*	*Thuja plicata*	*Tsuga heterophylla*	*Picea engelmanni*	*Abies lasiocarpa*	*Pinus albicaulis*
Pinus/Purshia (Keller)	.54											
Pinus/Purshia (Miles)	.45											
Pinus/Agropyron	.56											
Pinus/Symphoricarpos	.54	.56										
Pinus/Physocarpus	.65											
Pseudotsuga/Physocarpus	.69		.65	.35	.67							
Abies/Pachistima	.48	.70	.60	.30	.51	.59	.59*					
Thuja/Pachistima	.63		.65	.43		.59	.53	.33				
Thuja-Tsuga/Pachistima	.49		.50	.68	.41		.45	.47	.45			
Picea-Abies/Pachistima	.68		.58	.37	.38	.57	.57			.44	.56	
Picea-Abies/Xerophyllum										.58	.69	.44
Picea-Abies/Menziesia										.59	.59	.55
Highest value	.69	.70	.65	.68	.67	.59	.59	.47		.59	.69	.55
Lowest value	.45	.56	.50	.30	.38	.57	.45	.33		.44	.56	.44
Species average	.57	.63	.60	.43	.59	.58	.54	.40	.45	.54	.61	.50

*Value for a June collection at the same station: .63.

composited samples were included in this survey.

The litter was finely milled and digested with nitric and perchloric acids as described by Gieseking, *et al.* 1935. Nitrogen was determined by the Kjeldahl method (A.O.A.C. 1940), P by the method described by Griswold, *et al.* (1951), K was determined with a flame photometer, and Ca by the method described by Chapman (1928). The results are presented in Tables I to IV.

RESULTS

The only species consistently high in all four nutrients was *Populus tremuloides*—of the 12 species, it always ranked first or second, only *Larix* proving richer in P and *Abies grandis* richer in Ca. Among other species different constituents of the same tree varied from high to low to such an extent that it is difficult to rate them according to the quality of their foliage. *Pseudotsuga*, however, is second only to *Populus* in

TABLE II. *Total phosphorus as percentage of oven-dry weight of freshly fallen foliage*

Habitat types	Species											
	Pinus ponderosa	*Populus tremuloides*	*Pseudotsuga taxifolia glauca*	*Larix occidentalis*	*Pinus contorta latifolia*	*Abies grandis*	*Pinus monticola*	*Thuja plicata*	*Tsuga heterophylla*	*Picea engelmanni*	*Abies lasiocarpa*	*Pinus albicaulis*
Pinus/Purshia (Keller)	.09											
Pinus/Purshia (Miles)	.06											
Pinus/Agropyron	.07											
Pinus/Symphoricarpos	.12	.15										
Pinus/Physocarpus	.12											
Pseudotsuga/Physocarpus	.08		.15	.23	.05							
Abies/Pachistima	.08	.24	.14	.23	.04	.09	.10*					
Thuja/Pachistima	.10		.13	.24		.10	.07	.05				
Thuja-Tsuga/Pachistima	.08		.09	.17	.05		.06	.05	.17			
Picea-Abies/Pachistima	.09		.13	.18	.04	.08	.06			.10	.10	
Picea-Abies/Xerophyllum										.07	.09	.06
Picea-Abies/Menziesia										.08	.09	.08
Highest value	.12	.24	.15	.24	.05	.10	.10	.05		.10	.10	.08
Lowest value	.06	.15	.09	.17	.04	.08	.06	.05		.07	.09	.06
Species average	.09	.20	.13	.21	.04	.09	.07	.05	.17	.08	.10	.07

*Value for a June collection at the same station: .60.

highest average quality, ranking second in K, third in N, and fourth in both P and Ca.

The nutrient content of *Populus* leaves is similar to analyses made in other parts of North America as reported by Kittredge (1948), except that the K content is decidedly higher in this region.

One of the interesting results of the earlier phytosociologic study was a discovery that soils in the *Thuja/Pachistima* association are almost neutral, whereas those of the other three associations with the same ground cover are moderately acid. That the high Ca content of *Thuja* foliage is at least partly responsible for the high pH of the *Thuja/Pachistima* soils is also suggested by some data taken from Raney (Table V). Even in the relatively acid soils of the *Thuja-Tsuga/Pachistima* association there is a regular increase in pH and Ca content under the individual *Thuja* trees. An interesting feature is provided by the even higher Ca content of *Abies grandis* needles, for the soils of the *Abies/Pachistima* association are decidedly acid even though this association is usually adjacent to *Thuja/Pachistima* habitats. Apparently there are other influences of *Abies* upon the soil which prevent its high Ca content from raising the soil pH.

TABLE III. *Total potassium as percentage of oven-dry weight of freshly fallen foliage.*

Habitat types	Species											
	Pinus ponderosa	*Populus tremuloides*	*Pseudotsuga* tax. var. *glauca*	*Larix occidentalis*	*Pinus contorta*	*Abies grandis*	*Pinus monticola*	*Thuja plicata*	*Tsuga heterophylla*	*Picea engelmanni*	*Abies lasiocarpa*	*Pinus albicaulis*
Pinus/Purshia (Keller)	.20											
Pinus/Purshia (Miles)	.25											
Pinus/Agropyron	.65											
Pinus/Symphoricarpos	.33	.60										
Pinus/Physocarpus	.39											
Pseudotsuga/Physocarpus	.18		.60	.23	.33							
Abies/Pachistima	.33	1.78	.35	.40	.15	.35	.24*					
Thuja/Pachistima	.30		.38	.40		.35	.18	.20				
Thuja-Tsuga/Pachistima	.22		.32	.50	.20		.28	.38	.35			
Picea-Abies/Pachistima	.28		.30	.23	.13	.30	.20			.30	.25	
Picea-Abies/Xerophyllum										.23	.30	.18
Picea-Abies/Menziesia										.25	.23	.18
Highest value	.65	1.78	.60	.50	.33	.35	.28	.38		.30	.30	
Lowest value	.18	.60	.30	.23	.13	.30	.18	.20		.23	.23	
Species average	.31	1.19	.49	.35	.20	.33	.22	.29	.35	.26	.26	.18

*Value for a June collection at the same station: .20.

When the analyses are examined in relation to the lower of the two floristic discontinuities mentioned earlier, it may be seen that there is a difference in N content within those species which permit a comparison on both sides, but the difference is small in the face of the variability that might be expected, and no other nutrients show consistent trends here.

At the upper edge of the area supporting the *Pachistima* union, where the *Picea-Abies/Pachistima* forest is spatially replaced at higher altitudes on south-facing slopes by the *Picea-Abies/Xerophyllum* and at higher altitudes on north-facing slopes by the *Picea-Abies/Menziesia* associations, the abrupt impoverishment of the vascular flora is correlated with a pronounced reduction in Ca content of both *Picea engelmanni* and *Abies lasiocarpa* needles. The results here are so distinct, and the character of the ecotone so important that further comparative analyses of the few additional species that cross the ecotone are desirable. The data also show an increase in the N content of these two tree species where they extend into the impoverished flora, but Ca nutrition seems much more likely to be ecologically critical in the cold wet climates of these

TABLE IV. *Total calcium as percentage of oven-dry weight of freshly fallen foliage.*

Habitat types	Species											
	Pinus ponderosa	*Populus tremuloides*	*Pseudotsuga tax.* var. *glauca*	*Larix occidentalis*	*Pinus contorta* var. *latifolia*	*Abies grandis*	*Pinus monticola*	*Thuja plicata*	*Tsuga heterophylla*	*Picea engelmanni*	*Abies lasiocarpa*	*Pinus albicaulis*
Pinus/Purshia (Keller)	.39											
Pinus/Purshia (Miles)	.40											
Pinus/Agropyron	.30											
Pinus/Symphoricarpos	.56	2.35										
Pinus/Physocarpus	.53											
Pseudotsuga/Physocarpus	.80		1.04	.57	.54							
Abies/Pachistima	.31	2.03	1.88	.53	.55	2.14	.55*					
Thuja/Pachistima	.32		1.65	.49		2.66	.84	2.21				
Thuja-Tsuga/Pachistima	.36		1.67	.33	.73		.69	1.80	.60			
Picea-Abies/Pachistima	.31		1.61	.53	.73	2.54	.90			1.98	1.77	
Picea-Abies/Xerophyllum										.91	1.18	.19
Picea-Abies/Menziesia										.89	.78	.37
Highest value	.80	2.35	1.88	.57	.73	2.66	.90	2.21		1.98	1.77	.37
Lowest value	.30	2.03	1.04	.33	.54	2.14	.55	1.80		.89	.78	.19
Species average	.43	2.19	1.57	.49	.64	2.45	.74	2.00	.60	1.29	1.24	.28

*Value for a June collection at the same station: .60.

high mountain slopes. In Wyoming, Dunnewald (1930) also found the Ca content of *Picea* to increase with increasing pH of the soil and Chandler (1941) reports a similar relationship for *Acer* in New York, the Ca content of leaves rising sharply as the pH rises above 4.5.

In northwestern Europe, the Ca and N contents of conifer needles have been reported as showing weak correlation with forest site types (Aaltonen 1926, 1950, Ilvessalo 1923, Valmari 1921). However, a comparison of the composition of *Pinus ponderosa* from two *Purshia* sites, two *Physocarpus* sites, and four *Pachistima* sites shows that in the northern Rockies there is so much overlapping that correlation is feeble if if can be demonstrated at all in this species.

Other studies in progress indicate that within the geographic area to which these chemical analyses apply, the site potential for height growth of *Pinus ponderosa* is lowest in the *Pinus/Agropyron* habitats, little if any better in *Pinus/Purshia,* but uniformly high in *Pinus/Symphoricarpos, Pinus/Physocarpus, Pseudotsuga/Physocarpus,* and *Abies/Pachistima* habitat types. When these facts are studied in relation to the chemical analyses, no correlation can be found. Thus, the relationship between N content of foliage

TABLE V. *Means of soil analyses under 10 individual trees of Thuja plicata and 10 of Tsuga heterophylla growing in an old climax stand in Pend Oreille County, Washington. Ao layers removed before sampling. The t value for significance of differences of means exceeded the 5% level in all comparisons.* (After Raney 1948)

Depth in cm.	Tree	pH	Constituents as m.e./100 g soil			
			Extractable Ca	N	Oxidizable material	Ratio: Oxidizable material/N
0-5	Thuja	5.5*	46.7	3.98	41.2	10.1
	Tsuga	4.1	14.3	1.01	24.1	24.0
5-10	Thuja	5.8	39.4	19.4	147.8	7.60
	Tsuga	4.5	6.36	1.63	58.9	35.6
10-15	Thuja	5.9	34.2	17.4	121.7	7.00
	Tsuga	5.1	4.49	3.24	62.3	18.8
15-20	Thuja	6.0	35.4	5.25	62.1	11.8
	Tsuga	5.3	6.01	2.20	33.2	15.1

*Averages computed using equivalent arithmetic values.

and growth rate of *Quercus alba* in the Ohio River Valley (Anonymous 1951) finds no counterpart in *Pinus ponderosa* in the northern Rockies.

SUMMARY

Freshly fallen leaves of 12 species of trees native to the northern Rocky Mountains were analyzed for N, P, K, and Ca content. *Populus tremuloides,* the only dicot studied, produces litter that is definitely superior in average quality to that of any of the conifers.

The high Ca content of *Thuja* foliage may explain, in part, the regular increase in soil pH that is associated with this species, but the even higher Ca content of *Abies grandis* needles does not alleviate acidity in the *Abies/Pachistima* association, showing that Ca content is not a decisive factor.

Nutrient content is not related to site index for *Pinus ponderosa,* nor is it related to at least one of the forest site types in the area under study. The only exception is that there is limited but consistent evidence that the very acid soils of high mountain summits supporting *Xerophyllum* and *Menziesia* unions are correlated with reduced Ca content of those trees which extend up to such summits.

The general conclusion reached by many earlier workers that the chemical composition of tree leaves is primarily a characteristic of the species is borne out by this study.

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NOTES AND COMMENTS

NOTES ON THE BIOLOGY OF A SPINY LOBSTER, *PANULIRUS GUTTATUS*, IN BERMUDA[1]

Various records were kept on *Panulirus guttatus* during the course of an investigation of the biology of the common Bermuda spiny lobster, *P. argus*. Other than locality records in faunistic or taxonomic treatments, not much is known of the biology of this interesting little palinurid. For this reason, it is hoped that the following observations, covering the period of October, 1951, through October, 1952, may be of value. *Panulirus guttatus* was first reported from Bermuda by Verrill in 1922.

The animals were taken in lobster traps of local design (see Sutcliffe 1952) at various localities about the Bermuda plateau (Fig. 1), but most records were obtained from a trapping section including North Rock, Castle Harbor, and Nonsuch Island. Traps were maintained at depths up to 20 fathoms. All measurements are in terms of carapace length, in mm.

Panulirus guttatus is known locally as the

[1] Contribution No. 203 from the Bermuda Biological Station.

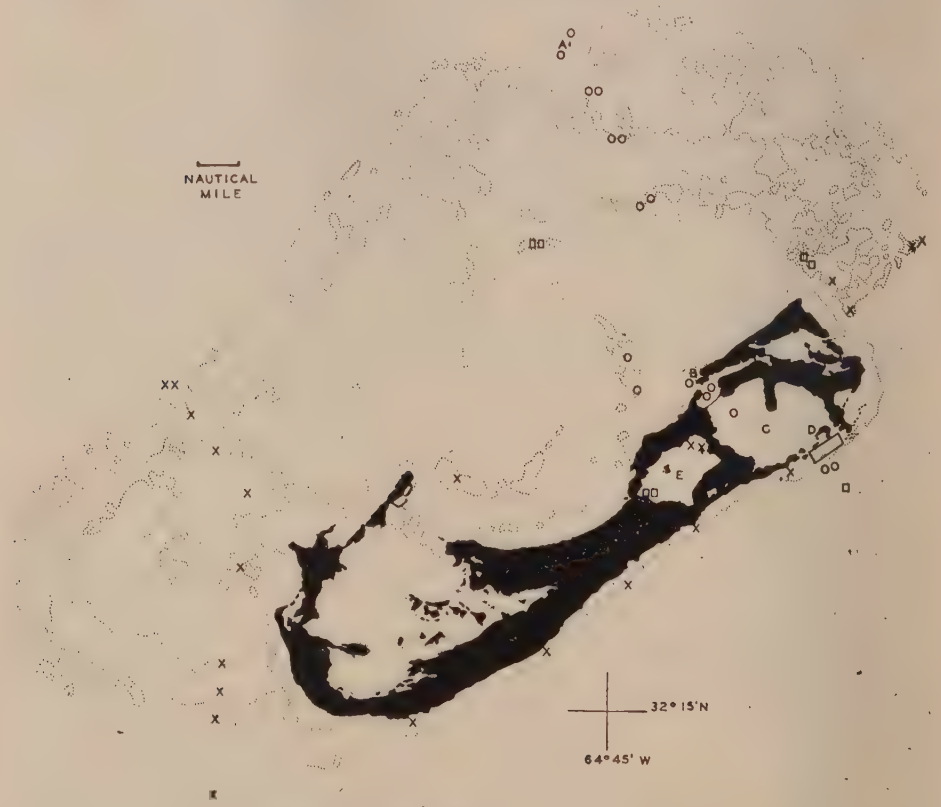

FIG. 1. Sketch map of Bermuda and reefs showing locations of traps:
Enclosed area represents seven or more traps maintained year round; isolated year round traps (O); maintained summer 1952 (x); maintained intermittently (□); North Rock (A); Whalebone Bay (B); Castle Harbor (C); Nonsuch Island (D); Harrington Sound (E). The dotted lines represent the three-fathom contour.

"guinea chick lobster" or "star lobster." Although nowhere really plentiful in Bermuda, it is sufficiently common to find a ready sale on the market, and is fairly frequently taken in traps located on the outer reefs. There it is found in a ratio of about one in twenty to *P. argus*. Unlike *P. argus* it does not seem to undergo any noticeable migratory behavior (Sutcliffe 1952), for it is seldom taken outside of a narrow band encompassing the outermost reefs or the relatively shallow water immediately adjacent. This agrees with the observations of local fishermen. Of 158 specimens examined during the period of observation, only two were found inside this reef area: one in Whalebone Bay and one in Harrington Sound. The latter specimen was caught behind the Government Aquarium and, according to Mr. Louis S. Mowbray, the Director, it was undoubtedly liberated there from the Aquarium a short time before. Adequate information is lacking regarding waters deeper than 20 fathoms outside the reefs, but in view of the very low catches per unit effort in 10 to 20 fathoms outside the reefs, as compared to the reefs proper, one wonders if occurrences in water deeper than 20 fathoms would be numerically significant.

Panulirus guttatus in Bermuda is a smaller species than *P. argus*. It may be seen (Fig. 2) that males much larger than 86 mm are not found, while in *P. argus* males attain a size well over 200 mm. If the size in the sample obtained may be considered indicative, the females are generally smaller, as with *P. argus*.

Of interest is the apparent considerable disparity in the numbers of the sexes. As seen in Figure 2, the ratio of males to females is about ten to one. This difference probably is not due to differential trapping effects, for the size of trap mesh used would retain a lobster somewhat smaller than 50 mm, while all of the captured females were 58 mm or larger. The few females taken were trapped well within the reef area already mentioned and were not restricted to any one season (see Table I). Although there is no evidence to indicate geographical or seasonal segregation, it is possible, nevertheless, that there is a localization of females somewhere on the Bermuda plateau. An interesting consideration is the possibility of differential survival of the two sexes inasmuch as Bermuda represents the northernmost known limit of this species.

TABLE I. Numbers of females of *Panulirus guttatus* with seasonal distribution and breeding condition.

Date	Bearing eggs	Having shed eggs	No signs of breeding
Oct. 1951.....	..	1	2
Jan. 1952.....	..	..	1
Feb. 1952.....	..	..	4
Apr. 1952.....	..	..	1
May 1952.....	..	..	1
Aug. 1952.....	1	1	
Sept. 1952....	..	2	1

Table I gives the available information concerning breeding. The one female with eggs was found in August, 1952; four females bearing a spermatophore remnant and showing signs of having carried eggs were taken in August, 1952, September, 1952, and October, 1951.

SUMMARY

1. The distribution of *P. guttatus* in Bermuda is relatively sparse and is apparently limited to the outermost reefs. This lobster is almost completely lacking in the lagoon and inside waters.

2. There is as yet no evidence of migratory behavior such as found in *P. argus*, the common spiny lobster in Bermuda.

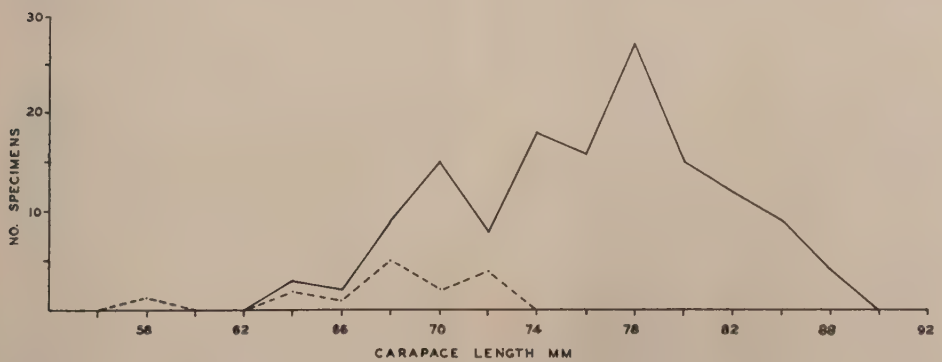

FIG. 2. Length-frequencies of *Panulirus guttatus* taken in Bermuda: females (-- - -), males (———).

3. Present data show a disproportionate sex ratio of about ten to one of males to females, and females are generally of smaller size.

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ARE OUR STEPPES BECOMING DRIER?

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[*Editorial note.* In reading this important paper by the late L. S. Berg, the American ecologist may be assisted by a summary of European postglacial stratigraphy. During and just after the maximum advance of the ice sheets of the last (Würm) glacial age, extensive deposits of loess were laid down in the drier and warmer parts of Europe and Siberia. This loess is hardly represented in Scandinavia and northwestern Europe, where the classical pollen stratigraphy has been worked out. Conversely, in the steppe regions where the loess is mainly found there is relatively little information about later events in the form of pollen sequences from bogs and lakes. The problem discussed by Academician Berg is therefore not a straightforward one of referring various sorts of evidence (pedologic, geomorphic, paleolimnologic, biogeographic) of arid or humid climates to the appropriate level of a standard pollen diagram; such a diagram does not exist for the region in question.

So far as the climatic history of northwestern Europe is relevant (and there are good reasons for believing it to be capable of world-wide application in its broadest outline), it may be considered tripartite (von Post, L. 1946. *New Phytologist,* **45**: 193-217). The postglacial climate was (1) increasingly warm, (2) reached maximum warmth, and (3) "deteriorated" or became cooler. Within (2), the postglacial thermal maximum, conditions were (2a) dry, Boreal; (2b) moist, Atlantic; and (2c) dry, Sub-Boreal. Phase (3), the Sub-Atlantic, was mainly moist as well as cool. The "xerothermic" time assumed by Berg may have been either (2a) or (2c), but was probably the latter, prevailing roughly from 2000 B.C. to 500 B.C.

A more refined stratigraphy of Swedish raised bogs (Granlund, E. 1932. *Sver. Geol. Unders., Årsbok* **26** (1): 1-193) shows at least five cyclic recurrences of dry and moist climates, each resulting in swamping of a previously dry and oxidized bog surface. The swamping times are dated on archaeologic evidence at 2500 B.C., 1200 B.C., 600 B.C., 400 A.D., and 1200 A.D., with the transition from Sub-Boreal to Sub-Atlantic ((2c) to (3) in the preceding paragraph) being the middle one (600 B.C., number III in Granlund's series of recurrence surfaces, which unfortunately is numbered from the youngest downward).

It follows that not all the evidence of former aridity discussed by Berg need necessarily be assigned to the Sub-Boreal ((2c), or the time just preceding Granlund's III). The deposition of the loess was almost certainly older, as Berg maintains, but Berg does not discuss the pos-

[1] Translated in slightly abridged form from the Russian by J. S. Joffe, Rutgers University, College of Agriculture. The paper appeared in *Pochvovedenie* (U.S.S.R.), No. 10, pp. 636-642 (1950).

sibility that the formation of solodi and the replacement of steppe by forest may by contrast be much younger, say 5th Century or even 13th Century A.D. What is especially confusing, and may have misled Tsyganov (whose work the writer cannot read) is that since about 1850 A.D. the dominant climatic trend has been opposite in character to the long-term Sub-Atlantic trend. That is, the climate has been getting warmer, especially in northern countries (and probably drier in some places) during the last century, whereas, despite such interruptions, it has been getting moister and cooler for the last two millennia. E. S. Deevey.]

Democritus claimed that our planet was becoming arid. A similar view was expressed by Kant. However, the majority of authorities maintain that the steppes have not become more arid during historic time. The following discussion is prompted by a claim of M. S. Tsyganov that since the ice age the steppe region is gradually becoming more arid. Tsyganov presents no new data to prove his contention.

With these preliminary remarks we shall proceed with a series of facts showing that our steppes have not become more arid during historic time. (For details and bibliography I am referring to my book *Climate and Life*, second edition, 1947.)

1. It was established by Gedroitz[2] (1912, 1928) that in the forest steppe and the steppes proper of the Chernigov region solonchak is being substituted by solonetz and the solonetz by solodi. This process can take place only under conditions of a climate changing towards greater humidity, the solonchak becoming free of salts and converted into solonetz, which upon leaching changes into solodi.[3] Gedroitz cites extensive distribution of solodized soils in the region of the Dnepr glacial tongue, in the chernozem belt of western Siberia at Yakutin. Apparently the solonchak that formed during the arid postglacial time turned into solonetz and solodi in our present-day more humid phase.

2. In the forest steppe, between the rivers Don and Volga in the hollows of the steppe watersheds, we find groves of aspen. At one time there was solonetz in the hollows. As a result of the changing climate, towards more humidity, solodization of the solonetz took place and tree vegetation made its appearance. "The aspen bushes," says T. Popov[2] (1914), "are only a particular stage of a complex process, the conversion of the watershed valleys into forest land."

An analogous phenomenon may be observed in the forest steppe of Western Siberia where the hollows are taken up, not by aspen, but by birch.

Both the aspen and the birch groves indicate the advance of the forest on the steppe. Incidentally, the mounds covered with aspen also indicate that. Among the solonetz, in the chernozem steppe near the Khrenovo forest (Voronezh region), solodi is found in the aspen groves. "They grow quickly and spread peripherally, which is obvious from the fact that younger trees are located away from the center. These forest-pioneers spread gradually, unite, and in that way the forest advances on the steppe." (G. F. Morozov,[2] 1930.)

3. In the xerothermic (Sub-Boreal) time the level of Lake Ilmen stood 1-2 meters lower than at present. This conclusion may be reached from the fact that at this level remnants of neolithic culture are found; also from the fact of the formation of podzolized soils in the deltas of Lovat and Msty (these soils are buried under recent deposits of alluvium and

[2] The references to Gedroitz and others quoted and not listed in the bibliography are to be found in Berg's book (1947). [*Translator.*]

[3] For a discussion of the terms solonchak, solonetz, solodi, and other pedologic terms, the reader is referred to *Pedology* by Joffe (1949). [*Translator.*]

swampy soils); also by the presence of peat bogs containing trunks of alder and birch (Sololov 1926, pp. 31, 214, 290).

4. Deep in the Siberian taiga, in the valley of the rivers Ket and Chulym (right tributaries of the river Ob), as well as in the Chulym basin, many sites of Neolithic age were found. In the little town of Ketsk (north of 58°) stone mattocks were unearthed. They represent evidence that in the Far North there were open spaces where agriculture was practiced (Kuznetsov, 1949, p. 146).

Kuznetsov (1949) studied the soils of the southeastern portion of the Western Siberian valley between the rivers Tomi and Yai, Yai and Kii, Kii and Chulym. He comes to the conclusion that the present climatic phase was preceded by a more arid one. At that time, the region of the present forest steppe harbored a steppe vegetation in association with halophytes and the soils probably were slightly salinized. This may be inferred from the fact that the grey podzolized soils that prevail now show no signs of salinization, but contain in their humus horizon free amorphous silicic acid up to 2% (pp. 178-180). According to Gedroitz, free amorphous silicic acid is not found in the upper horizons of normal unsalinized soils, at any rate not in quantities exceeding 0.1%. However, in soils that have gone through the stage of salinization the quantity of free amorphous silicic acid may reach appreciable quantities. Thus, 6.6 to 12.7% of free amorphous silicic acid is reported for solodi. Kuznetsov comes to the conclusion that the grey podzolized soils and slightly podzolized chernozem in the western Siberian region were at one time weakly salinized. Again, according to the data of K. P. Gorshenin,[2] the chernozem soils of western Siberia are genetically related to the solonetiz soils; and E. N. Ivanova[2] (1930) maintains that the podzolized soils of the western Siberian forest steppe are solodized. In the upper horizons of these soils there is up to 1.5% and more of free amorphous silicic acid, whereas in the normal chernozem there is only $\frac{1}{10}$ of that amount (compare Berg 1947, p. 336).

A. Ya. Bronzov[2] (1936) studied the peats of Vasyugansk swamp located in the watershed of Irtysh and Ob. The southern part of the swamp is covered with sedge peat. The northern part is covered with sphagnum. The sphagnum peat formed in the watershed areas primarily during the last two thousand years. The sphagnum peat, as a rule, does not effervesce at the surface upon the addition of acid. In the sedge peats of the Narym region, the underlying parent material usually effervesces from the top, seldom lower than from a depth of 10-15 centimeters (p. 239). Before the formation of these bogs there was surface-effervescing solonchak which contained chlorides and sulfates. Bronzov postulated that in the taiga region investigated, the border between the forest steppe and the steppe proper passed through the Ob-Irtysh watershed during the xerothermic time. This border approximately corresponded to the border that separated the sedge steppe of the Vasusyugansk from the sphagnum which is located farther north (p. 241).

The solonetzic properties of the chestnut-brown soils indicate a degradation that took place in a previous arid phase. These soils were then more saline, but in the present time of more humid climate they have been leached of their salts, thus transforming into solonetz (Gerasimov and Markov 1941, p. 25).

In the upper layers of the lake-bottom deposits (sapropel) of the freshwater Kamyshlov lakes in Hinter-Ural, we find the modern fresh-water diatoms. At lower levels, however, salt-water forms prevail. This means that at one time the lake waters were more concentrated. The salinization of Sheshukov at that time proves that a more arid and warmer climate existed at the time when the deeper mud was forming. Similarly, in the bottom deposits of the fresh mountain lake Uvild in the Urals, brackish-water dia-

toms have been observed, which seems to indicate that the lake was formerly saline. On these deposits, which A. P. Zhuze (1939, p. 47) places in xerothermic time, there are freshwater precipitates of the Sub-Atlantic phase. Below the saline water horizon there is a layer containing fresh water diatoms. Therefore, the original fresh-water basin became brackish, and then became fresh once more, remaining in this condition until today (see Zhuze p. 46, diagram 10).

According to data of Sukachev and Poplavskaya (1946, p. 34) the lakes of the dissected peneplain and the Tertiary valley in the region of the Central Urals apparently have completely dried up during the xerothermic phase. They began to accumulate deposits of sapropel only after this phase.

One may fully agree with K. A. Kuznetsov's conclusions on the territory of western Siberia investigated by him (1949, p. 186):

"Paleographic, archeologic, historic, and soil data show that our region was characterized by an arid and relatively warm climate in postglacial time. Under these conditions steppe vegetation prevailed, including halophytic forms. Under such plant cover, chernozem soils and some varieties of these, such as solonetzic and solonchakic soils have developed. In the historic period, the climate has changed towards greater humidity and lower temperature. As a consequence the vegetation zones have shifted from North to South, and our region became covered with forests under which the inherited chernozem soils began to change and were converted into podzolized soils."

We have purposely devoted much attention to the vegetation zones of western Siberia because this region gave Tsyganov the basis for his assumption that there is progressive aridity of our climate.

M. S. Tsyganov accuses the investigators of western Siberia "of faulty interpretation of the geologic history which allows the existence of a xerothermic phase, with dry and hot climate, after the glacier retreat."

However, nobody talks of a hot climate in western Siberia. What is meant is a relatively warm, dry climate. During one of the intervals of postglacial time western Siberia had a drier and warmer climate than at present. No one doubts that, as we have seen. In western Siberia one may clearly see how the climate is gradually becoming more humid so that the forests are advancing on the steppe.

5. A change in climate of western Siberia in the direction of greater humidity can also be inferred from topographic data. An examination of the map of Lake Chana in the Barabinsk steppe convinces one that the waters of this lake occupy a basin that was only recently filled. One may judge this from the *rias*-form of the lake shore, with its long and narrow peninsulas and bays extending from Northeast to Southwest. The peninsulas represent crests and the bays represent drowned ravines. Northeast from Chana, near the tracks of the Siberian railway, lies Lake Ubinsk. Its basin, no doubt, was also dry at one time. On the bottom of the lake there is a bank which represents a continuation of the Kargat ridge which follows the right bank of the River Kargat (Berg 1947, p. 105). In a similar fashion, the forms of the Aral and Caspian shores clearly show that these seas have raised their level in recent times (p. 108).

6. The advance of the forests on the treeless areas may also be observed in eastern Siberia. We shall cite one example. On the watershed between the Lena and Amga rivers we find solodi (Krasyuk and Ognev,[2] 1927), the parent material of which is a loess-like loam rich in carbonates. These solodi are covered with larch or birch-larch forests. The course of events in this area was as follows:

(1) Formation of a loess-like loam during the arid postglacial time.
(2) Formation of solonchak.

(3) Leaching of solonchak and conversion into solonetz and finally into solodi.
(4) Invasion and final coverage of the solodi by forests.

7. We shall turn our attention now to the European forest steppe. Gedroitz[2] in his famous work on the solodization of soils (1926) presents an acceptable supposition that the present-day non-solonetzic, relatively inorganic chernozem type of soil in the region of the Dnepr glacial tongue represents a solodization of the carbonate solonetzic soils. Such a solodization is associated with an intensive leaching which means a more humid climate. We may add that the solodization of solonetz takes place rather rapidly.[4]

The advance of the forest on the steppe may be beautifully observed in the Miussk forest stand on the Don heights. At the edge of the forest which consists of oak and ash, shrubs such as blackthorn, dog-rose, hawthorn, and cherry are found. Beyond the edge of the forest these shrubs form isolated groves in the steppe. In the course of succession in such groves trees make their entry, such as the Tartar maple, pear, and apple, followed by ash and finally by oak. Only in recent times have many of these shrub-groves been converted into sizable forest groves uniting gradually with the continuous forest stand. That the forests are advancing on the steppe is also apparent from soils data; the degree of degradation of the soils decreases from the center of the forests towards the periphery. The vanguard of the forest occupies districts of non-degraded chernozem (Berg 1947, p. 349).

8. It is known that in eastern Europe a process of substitution of oak by pine goes on. This phenomenon has been noted in Poles'e, not far from Moscow, in the basin of the river Vetlug, and in other places. I agree with G. F. Morosozov that the replacement of oak by pine is associated with a change toward a more humid climate (Berg 1947, pp. 247-248, 255-256).

In historic times, the Alpine glaciers have not descended the flanks of the mountains so far as they did about 1600, 1820, and 1850 (Wagner 1940, p. 66). Here is one example: in the region of Mont Blanc, in the year 1605, two small villages were destroyed by advancing glaciers. This shows that the quantity of precipitation in the 17th and 18th centuries and in the first half of the 19th century has increased in comparison with prehistoric times. A similar picture has also been observed in connection with the glaciers of Iceland (Wagner, p. 66).

9. That there was an episode soon after the ice retreat with a drier climate than at present and with summers warmer than today nobody can dispute. Striking evidence of this may be found in the fact that chernozems have formed on loess-like loams. Whatever theory one may adhere to in explaining the origin of loess, all investigators agree that loess and loess-like loams were formed during an arid period. Evidence of this may be found in the fact that these parent materials contain carbonates and very little organic matter. The presence of chernozem on loess parent material also indicates a change in climate towards more humidity.

No one denies that there was an arid episode during postglacial time. The question is, however, to which arid phase belongs the period of loess formation? Does it belong to the period following immediately after the retreat of the glaciers, as we think, or does it belong to the Sub-Boreal phase which began before the time of Christ?

10. It is possible to adduce a great deal of historic evidence pointing to the fact that during the Christion era the climate of the U.S.S.R. has not changed towards a decrease in humidity. On the contrary, there is a series of facts which indicates a change in the direction of greater humidity. I shall just present a few facts, and for details I refer the reader to the

[4] For a discussion of this point the reader is referred to Joffe (1949, pp. 325-327, 582-585). [*Translator.*]

literature of my book "Climate and Life" (1947).

As early as 1857, K. S. Veselovskii, in his monograph "On the climate of Russia," had a chapter: "Has the climate of Russia changed during historic time?" Comparing the statements of Herodotus, Ovid, Strabo, Pliny, and others with the ideas and data of our own day, Veselovskii comes to the conclusion that the climate of Russia has not changed towards aridity during historic time. On the basis of studies of the chronicles beginning with the 11th Century, M. Bogolepov[2] (1907) had established for European Russia only slight fluctuations in the climate that might last a couple of decades; there is no evidence of progressive aridity.

A great many historic data may be presented to corroborate the idea that Soviet Central Asia has not experienced increasing aridity during historic time. Arrian, an author of the 2nd Century who compiled the history of the campaigns of Alexander the Great, shows that in the 4th Century B.C. (328) the Zeravshan (Politimet) did not reach the Amu-Dar (as it doesn't now). "Alexander the Great passed through the entire country which was irrigated by the Zeravshan. At the point where the river disappears, the country takes on the appearance of a desert. Notwithstanding the huge quantity of water, the river disappears in the sands. In similar fashion, a great many other rivers are being lost (among the later, Arrian names the River Arii which is now known as Geri-Rud or Tedzhen). This is also corroborated by Strabo. "The river Politimet enters a sandy country and is swallowed up by the sands as it happens also with the river Arii in the land of the Arians." In the 10th Century, in the time of the Arab historians, the river Zeravshan is described in the same manner. It should be added that only in 1874 have the waters of the Zeravshan reached the Amu-Dar. According to data of Istakhri, an Arab geographer of the 10th Century, the waters of Geri-Rud (Tedzhen) in low-water seasons did not reach Serakhs. The Aral sea coast has now the same position that it had a thousand years ago.

These examples show that Turkestan did not have more water two thousand years ago than it has now. This kind of evidence can be multiplied considerably.

In fact, the sandy deserts of central Asia are not present-day formations. If left undisturbed, the shifting sands of this country quickly become covered with vegetation. Therefore, the sands that are now stabilized, which at one time were shifting, formed not in our time but during one of the postglacial arid phases. The same may be said of the sands of the shores of the Ukrainian rivers; they also are being covered with vegetation.

Conclusions

There is no evidence pointing to a progressive aridity of our steppes and deserts. On the contrary, there is reason to believe that the present climatic phase of postglacial time is more humid than the preceding arid or xerothermic interval.

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DIFFERENCES BETWEEN MEASUREMENTS OF LIVING AND PRESERVED AQUATIC NYMPHS CAUSED BY INJURY AND PRESERVATIVES

Many attempts have been made to determine the growth of populations of aquatic insects by making measurements of certain body dimensions of the individual nymphs. Probably the most used measurement has been that of body length.

While trying to determine the growth rate of the mayfly, *Ephemera simulans* Walker, in Lake Erie, it was found that body length of some preserved specimens varied greatly from body length of live specimens. The variation appeared to be very pronounced if the specimens had been injured. This was also true, however, in some cases where no injury was apparent. The nymphs had already been killed and fixed in KAAD (Peterson 1948, p. 6) and preserved in 95% alcohol. Therefore, in order to get a reliable index of growth, it was necessary to find some structure on the nymphs that was easy to measure and showed little change when preserved.

To estimate the differences between measurements of live vs. preserved specimens, two groups of live *Ephemera simulans* nymphs were collected. In the first group of 23 live specimens, four measurements were made of each. These were killed and fixed in KAAD for 24 hours then transferred to 95% alcohol. After 7 to 10 days they were again measured, and the results compared with the first measurements. The second group of 20 specimens was treated in the same manner as the first group, with one exception. Each specimen after being measured alive was injured by slightly crushing the thorax or abdomen or by piercing the body with a pin to simulate injuries which occur while making regular collections.

The average of each of the four measurements in each group is given in Table I.

The table shows that the total length variation is several times greater than that of the other measurements. On uninjured specimens KAAD has a tendency to slightly increase the length, while injured specimens become greatly telescoped, thus giving an average difference in length of 16.51% (4.18% + 12.33%) between the injured and uninjured preserved specimens. Rostrum length and eye diameter show only small variations, but are difficult measurements to make because of size and indefinite index points. The head width in these specimens is easy to measure and is large enough to give reliable data. Also, the head width shows very little variation. The head of a mayfly nymph is heavily chitinized and more or less fused together; therefore, it is not surprising that it should show less variation than the soft parts such as the thorax and the abdomen. However, another study, not yet completed, shows a general correlation between head width and body length. By using head width instead of body length, the measurements of the injured specimens are as reliable as those of the uninjured. This is especially important where the collections are small.

It was concluded that, for *Ephemera simulans* specimens killed in KAAD and preserved in 95% alcohol, the head width offered a more

TABLE I. Average Measurements (in mm.) Made on Two Groups of *Ephemera simulans* Nymphs Before and After Being Killed and Preserved.

	Eye diameter	Rostrum length	Head width	Total length
23 Uninjured Specimens				
Living	.5890	.6224	1.4006	15.697
Preserved	.5979	.6290	1.3808	16.353
Difference	.0089	.0066	.0198	.656
Difference as per cent of live measurement*	−1.51	−1.06	+1.41	−4.18
20 Injured Specimens				
Living	.5941	.6626	1.3839	15.560
Preserved	.6137	.6528	1.3863	13.642
Difference	.0196	.0098	.0024	1.918
Difference as per cent of live measurement*	−3.30	+1.48	−0.17	+12.33

*Negative differences indicate that living specimens were smaller

reliable index of growth than did the other measurements. Total length was found to be the least reliable.

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PALYNOLOGY AND THE THORNTHWAITE CLIMATIC CLASSIFICATION

The main purpose of pollen analysis, or palynology, is to determine the climatic sequences during a given period of sedimentation. Since designation as precise as possible of climatic intervals is important, and since the pollen of forest trees is the main index to past climates, it was suggested to the writer by Professor Paul B. Sears that the ranges of certain trees whose pollen is important in North American profiles be mapped in terms of the Thornthwaite system of climates.

The present range of each species was considered to mark the greatest natural extension possible under present climatic conditions. By comparison of the range maps of the various species (Munns 1938) and the climatic maps of the United States (Thornthwaite 1948) and Canada (Sanderson 1948), it was then determined under which climatic types each species is found. The climatic characteristics of each species were summed up in a series that denotes the only climatic conditions in which the species could be expected to occur. This series is later referred to as "the series of possible climates." For instance, *Fagus grandifolia* Ehrh. currently grows under A—C_2; B'_4—C'_2; r and s; a'—b'_1; *Carya cordiformis* (Wang.) K. Koch A—C_1; B'_4—C'_2; r, s, and d; a'—b'_1; and *Picea glauca* (Moench.) Voss A—C_1; B'_1—D'_1; r, s, and d; b'_2—d'. Generic characteristics were determined by compositing the characteristics of the respective species.

From the species and genera present at a particular level in a pollen profile, from the fact of their presence alone, a summation of the climatic characteristics of the individual species and genera can be read off as the series of possible climates for that level. Important to note is that nothing is said about the actual climate; only the question of possible climates is dealt with. It can be said that the climate at the given level must have been between the extremes of the series of possible moisture and thermal conditions; it definitely cannot be said what the actual climate was at the given level (time) in the specific locale from which the profile came merely from a list of the species and genera present. But the climate in any particular locale at a given time, if known, can be classified more or less exactly by the Thornthwaite classification, *e.g.,* San Francisco, California, $C_1B'_1s_2a'$, and Bar Harbor, Maine, $AC'_2rb'_2$.

No difference in the series of climatic possibilities appears between the case in which species X and Y are present with X dominant, and the case in which species X and Y are present with Y dominant. If several species or genera are constantly found in a profile, clear trends indicating corresponding changes in climate are not reflected in the series, which stays the same, *i.e.,* shows the same possible climates, throughout this profile because the same species and genera are found at all levels. Change in the series of possible climates can be shown only if a species or genus drops out entirely or appears for the first time, or reappears. This change in the series need not necessarily reflect the actual climatic change. Clearly then, the Thornthwaite classification helps determine the climate from pollen profiles only in that the extremes within which the climate must have been can be fixed. Nothing can be observed directly about the actual climate at a given time or about the changes in climate.

Until present knowledge about climatic relations and the autecology of the present species is amplified, it seems best that use of climatic generalizations (*e.g.,* cold-wet, warm-dry) be continued in preference to substituting climatic classifications of the Thornthwaite type. The climatic generalizations are more helpful in that they suggest the habitat characteristics; the classification can give only a hint of the actual climatic fluctuations when the series of possible climates is determined from a list of the genera and species found in a profile. Greater delimitation is necessary, of course. Perhaps the actual climate can be determined, within the series, by consideration of the autecology and synecology of the species in the profile. Use of the climatic classification would serve only as a guide by setting up extremes within which the climate must have fallen. However, whatever usefulness the classification might so have is diminished by the fact that the extremes set up are so wide apart that, in effect, little help is given toward a close determination of the history of climate.

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ANALYSIS OF GEOTACTIC RESPONSES IN *DAPHNIA MAGNA*

The work of Smith and Baylor (1953) suggests a number of further experiments on the color responses of Cladocera. Of immediate interest is the origin of the gravity stimulus through which the geotactic response to a color change is possible. The presence of mixed geotaxes and phototaxes in the light responses of these organisms has long been recognized (*e. g.*, Clarke 1930; Dice 1914).

A direct study of the geotaxis is made possible by the use of a colored light stimulus which elicits a pure geotactic response. With organisms adapted at least 15 minutes to a given light, any shift in the proportions of long (over 550 mμ) to short (under 450 mμ) wave lengths toward shorter wave lengths, but with no change in apparent brightness to the animals, produces a positive geotaxis, regardless of the direction of the light beam. (The reverse stimulus, shifting after 15 minutes toward longer wave lengths without a change in apparent brightness, produces not a negative geotaxis, but a positive phototaxis.)

A pair of color filters producing a shift in wave length without a change in apparent brightness was chosen in the following way. A one-gallon tank containing Daphnia was set up with identical parallel beams (Spencer microscope lamps) shining in from opposite sides. Both beams of light were filtered with a matched pair of yellow filters (Corning #3482), and the diaphragms of the lights adjusted until, after several minutes, the population was divided equally between the two lights. (If one of the light beams were brighter to the Daphnia than the other, the population would have moved gradually towards the brighter light source.) The filter at one side was then changed to a combination of two blue filters (Corning #4303 and #5113), chosen for the completeness with which all light stimulating the "yellow sensitive receptor" in the cladoceran eye is filtered out. A series of yellow to red filters was then tried in the other beam of light, until one was found for which the animals would divide between the two lights equally. An orange filter (Corning #3480) was found satisfactory. It happens also to filter out all of the wave lengths which stimulate the "blue sensitive receptor" in the cladoceran eye. Although these filters are of equal brightness to the Daphnia, the orange filter, to the human eye, appears to be several times brighter than the blue filter.

Geotaxis is best observed using a wide parallel beam of light entering from the side. After the orange filter (Corning #3480) has been in place for 15 minutes, a change to the combination blue (Corning #4303 and #5113) produces a vigorous and protracted downswimming throughout the population. (If the color change is made before the animals are fully adapted to the orange light, there will occur a negative phototaxis at the same time as the positive geotaxis, and hence, diagonal motion is produced.)

While a light stimulus elicits the geotaxis, the animal must have available some mechanism to denote the direction of gravity. Although no internal receptor has been described, an experiment to determine whether the receptor is internal or external was deemed necessary. The density of the animals is greater than that of water, and it is possible that they determine the direction of gravity by sinking between swimming strokes. Such an orientation would be reversed if the animals were placed in a solution with a specific gravity so high that they "sink" upwards. If the receptors were internal, however, orientation for geotaxis would not be reversed in this way.

A 13-15% solution of sucrose was found to be optimal for creating the desired change in specific gravity. In it, the Daphnia tend to rise about as rapidly as they ordinarily tend to sink. Although the osmotic pressure is greatly increased, the animals behave normally for at least 15 minutes, after which their motions become erratic as osmotic death approaches.

A tank of *Daphnia magna* containing pond water was set up as a control, and to serve as a reservoir in which the organisms could be pre-adapted to the wide orange beam of light from the side. A tank of the sucrose solution was placed next to the control in the same beam of light. After a suitable adaptation time interval, several animals can be moved to the sucrose tank; and after allowing a few minutes

more for recovery of the Daphnia from the disturbance, the color change from orange to blue can be made.

When the light is changed from orange to blue, the control animals swim straight down as would be expected, while the animals in sucrose swim straight up. On the reverse change of light, the animals in both tanks swim straight towards the light. With many other light stimuli, Daphnia in the sucrose solution always behaved exactly like those in normal water, but with a reversed orientation to gravity. With no change in light at all, those in sucrose swim about quietly, upside down.

Since in all respects the gravity orientation is reversed by a reversal in the density relations between the organism and the medium, it would appear that the gravity receptor is external, and is determined by a tendency to sink.

High-speed motion pictures of swimming Daphnia show that the down stroke of the antennae is accomplished in a small fraction of the swimming cycle, and that the return stroke is half as fast; but, for the major portion of the cycle the antennae are up, outspread, and motionless. During this brief period of sinking between strokes, the gravity stimulus may stem either from stress on the antennae or from stress on the many small hairs of the antennae. While evidence from a single injured specimen that had lost its hairs favors the latter hypothesis, a more positive decision awaits further investigation.

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THE ROLE OF LICHENS IN SOIL FORMATION AND PLANT SUCCESSION

Plant ecologists frequently state or imply that various species of lichens and mosses are the pioneer plants in simple successions on rocks,[1] and that they initiate processes which apparently result in the destruction of the rocks and the formation of soils in which higher plants can grow. (*e.g.*, Clements 1904, Cockayne 1908, Braun 1917, Frey 1922, Whitehouse 1933).

Descriptions of the supposed role of lichens in soil formation and/or plant succession from two recently published textbooks, are quoted below:

"The initial conversion of rock into soil is carried on by the pioneer lichens and their successors, the mosses, in which the hairlike rhizoids assume the role of roots in breaking down the surface into a fine dust."

(Clements and Shelford 1939)

"The crustose forms are the world's great pioneers. No organism other than a crustose lichen can maintain itself on a perfectly plain, clean rock surface. These plants are, therefore, of exceptional significance as forerunners of other kinds of life in rocky places. During the long period of development of a crustose lichen on a rock surface the mycelia of the fungus often pry into crevices, gradually breaking loose small particles. In some cases secretions from the cells of the plant dissolve parts of the stone. In addition, dust often lodges on the surface of the lichens and with death of its older parts, minute bits of humus are formed. The mixture of sand, dust, and humus may become a trace of loamlike soil in which other small plants can live. Most often these are some of the hardier mosses. With their growth and death still more soil becomes organized and larger plants may take root in it. Without the pioneering activities of crustose lichens other plants could become established slightly or not at all in many places."

(Emerson 1947)

From these accounts it would appear that the pioneer lichens initiate important processes of rock disintegration and soil formation, and are the forerunners of other kinds of plant life in rocky places.

In popular scientific articles the role of lichens is frequently mentioned. For example, in the guide book to Crater Rim Trail, Capulin Mountain National Monument, New Mexico, issued by the Southwestern Monuments Association of Santa Fe, New Mexico, the tourist is invited to pause at Station No. 25 to observe "green and yellow lichens and green

[1] The term rocks is used in reference to rock faces and rock crevices indiscriminately in this paper.

moss: two steps in the unfolding of a story called 'plant succession' (the breaking down of rocks into life-supporting soil)." In *Life* of December 8, 1952, pp. 94-5, green dabs of lichen are shown clinging to the primeval rocks of the recently born earth and are described as one of the earliest forms of life. In the same magazine of December 29, 1952, it is stated that the vegetation of Mars is probably lichens.

Doubts regarding the role played by lichens and mosses in soil formation were roused in the mind of the senior author when he witnessed the eruption of Mt. Ngauruhoe, New Zealand, in February, 1949. The eruption began on 9 February with the discharge of large blocks of hot lava from the crater. Lava emerged on the following day and streamed down the north-west slope of the cone. The eruption of ash clouds followed the lava phase and continued until the beginning of March. The quantity of dust and sand stirred up by the falling rocks, produced by the movements of lava and erupted during the ash phase, was considerable. A surface layer varying in depth from several inches to several feet covered the lower north-west slope of the cone on 11 February, before the main ash clouds were produced, but much of it had been blown or washed into crevices when the mountain was visited again in May 1949. Many of the large blocks of hot lava, ejected during the first phase of the eruption, spalled down into small pieces as they cooled (Battey 1949), and the resulting debris was considerable.

Possibly much of this dust and debris is sterile, and drainage in this material is very rapid, but it seems that a lichen-moss stage will not be necessary before seed plants migrate to crevices in the lava flow (R. Cooper 1949). On Mount Capulin it was observed that the cone consists of scoria cinders and ash on a base of lava flows, and again it is unlikely that a lichen-moss stage played any important role in the formation of soil.

Another similar area of bare ground in process of colonization is Rangitoto Island, a volcanic cone in Auckland Harbour, New Zealand. According to Cockayne (1928: 107), every stage of plant-colonization can be seen here, from occupation of rocks by lichens, liverworts, mosses and even *Hymenophylaceae* to actual forest. But the island is built of lava flows capped by a central cinder cone, and again it is evident that the soil found in the crevices in the lava has been formed from dust from the cinder cone as well as from the decay of lichens.

In the course of the field study of lichens, the junior author began to question the classical succession from crustose lichens to higher plants. A rapid survey of recent literature showed that other students had somewhat similar doubts, *e.g.*, McDougall 1949, Conard 1952. In a few ecological studies the authors describe successions on rocks in which the crustose and foliose lichens present play no vital role in the succession, *e.g.*, Oosting and Anderson 1937, Keever, *et al.* 1951. The latter authors state explicitly that: "In every instance, the first plants to appear on rocks are crustose and foliose lichens, but in no places are they found to be essential to further development."

Measurements of the rate of growth of lichens on rock surfaces show that they spread very slowly (Fink 1917, Smith 1921, W. S. Cooper 1928, Hausman 1948). A few studies demonstrate that the sequence from crustose to foliose and fruticose lichens is not constant, and the extensive Scandinavian literature indicates that succession within lichen communities is not simple. Furthermore, rock faces of great age are sometimes found which have been invaded by lichens but which apparently have never been covered with other vegetation. The evidence they provide is essentially negative and we have the impression that it is usually ignored.

The role of lichens in disintegrating rocks has been investigated by a number of lichenologists who found that lichens cause some damage to certain rock surfaces, but the amount is comparatively slight (Bachmann 1904, 1911, 1917; Fry 1927). The remarks of Keller and Frederickson (1952), on the part played by colloidal acids in weathering refer particularly to the roots of higher plants. Furthermore it is noted that in three recently published text books on soil there is no mention of lichens and mosses playing a role in the destruction of rocks and the formation of soils (Jenny 1941, Lyon and Buckman 1943, Weir 1949).

There is ample evidence that lichens and mosses invade bare rocks, collect and hold water and dust, and decay. The work of certain authors shows that mosses, and some foliose and fruticose lichens which are mat-formers, accumulate debris at a more rapid rate than crustose lichens (W. S. Cooper 1912, Oosting and Anderson 1937, Keever, *et al.* 1951). We believe however that the importance of these processes in plant succession and in the development of soil has been exaggerated greatly in some ecological studies, botanical textbooks, and popular science articles. The evidence available to us strongly suggests that the presence of lichens is not always an indication of the beginning of a succession and is not essential to the formation of a soil and the development of vegetation in rocky places.

Summary

The classical role of lichens in soil formation and plant succession in rocky places is ques-

tioned and evidence is presented to show that the importance of lichens has been exaggerated and that the developmental story of the vegetation has been over-simplified.

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The Tropical Rain Forest[1]

This is an important book. It is the sort of book that initiates a new period of development in its field. It is a wisely conceived, carefully prepared treatise, monographic in scope and written in a clear straight-forward and pleasing style. It is doubtful if any other biologist could have produced a book treating the rain forest with such range and comprehension and larding the text with such a wealth of hitherto unpublished information.

The scheme of organization is practical and reasonable. The 17 chapters are divided among five parts and an important introduction, and these are followed by a postscript, a 15-page list of references, an index of plant names and a general index. The photographic illustrations are on the whole excellent, and the graphic, diagrammatic and tabular devices are sound, clear and pointed.

The introduction (ch. 1) is a generalized essay on the tropical rain forest as a climax plant association. The formation-type is defined in broad terms, its biological spectrum discussed and its geographic subdivisions recognized. There is an appraisal of the status of current knowledge of the rain forest and an effort is made to correct some of the widespread misapprehensions that the average book on tropical travel conveys. The airing here of the inadequacy of our understanding of this most exciting of all biotic communities will surely have a salutary effect. It will come as a surprise to some readers that even the more elementary descriptive aspects of rain forest ecology remain largely undeveloped. There are not even, for instance, any really decent maps of the world distribution of rain forest.

Professor Richards calls attention to the anomalous attitude of the many botanists who regard the tropical rain forest as an aberrant, abnormal and highly specialized community, whereas actually it is almost surely the prototype of modern forests and the original home of the broad leafed evergreen tree which is in turn the type from which most other flowering plants have derived. He reasonably suggests that studies of tropical vegetation ought to be more productive of fundamental principles than work in temperate areas and deplores the fact that "tropical vegetation is still so little known that its significance for ecological science in general can be only dimly seen."

The introduction is concluded with the author's interpretation of the extreme floristic richness of the tropical rain forest as merely an expression of the antiquity of the formation, which "has been a focus of plant evolution for an extremely long time." I believe that this is perhaps an oversimplification. It seems more likely that the diversity of tropical forest life is the result of the interaction of a number of factors, and seems just as certain that the systematic study of these promises huge rewards to the student of evolution (see Dobzhansky 1950. Amer. Scientist, 38(2) : 209-221).

In Part one (ch. 2-5) the rain forest is treated from the standpoint of structure and physiognomy, and it is here that the master hand is most evident and the author's own background and interests perhaps most freely tapped. Stratification, one of the salient features of the tropical evergreen forest, is here discussed in all its aspects. There is a thoroughly modern section on the subject of regeneration, in which serious attention is given the possibly very significant theory of "mosaic regeneration" which may one day completely disrupt the current concept of the static climatic climax. Although perhaps not applicable to all kinds of rain forests in all regions, there can be little doubt that the mosaic theory has wide relevance and is an important step toward a grasp of succession dynamics and equilibrium in tropical communities.

There is in Chapter 4 a remarkably exhaustive treatment of the generally slighted subject of the structure, development and habitat relations of buttresses in forest trees. In this excellent review there occurs what I believe to be one of the very few factual errors in the book when toward the bottom of page 65 we are told that buttresses are absent in montane forest trees. This is far from being the case, since some of the oaks and lauraceous components of the Central American cloud forests are as drastically buttressed as any but the most extreme examples among rain forest trees.

Moreover, I am unable to follow Professor Richards' partitioning of morphologic features as either "adaptional" or causal" and sense an unpromising Lamarckian implication in the latter category; but this is mere quibbling, and the real point here is how pitifully little evolu-

[1] **Richards, P. W.** 1952. The Tropical Rain Forest, xviii—450 pages; 15 plates; 43 text-figures. New York: Cambridge University Press. $12.50.

tion has been studied in the field. This essay on "ecologic morphology" is on the whole an extremely valuable contribution, which could not fail to interest and instruct any biologist with a leaning toward the tropics.

Part two (ch. 6-9) is concerned with the rain forest as an environment. There is an account of the physical factors of climate and microclimate, a chapter on seasonal changes, and the best summary of rain forest soils since that of Vageler.

Part three comprises two chapters (10-11) on the floristic composition of primary rain forest. Various regional types are described and the general subjects of mixed-, single-, and family-dominance taken up. In a summarizing "theory of the climax" Professor Richards finds little support for a rigidly defined monoclimax state in either soil or vegetation successions, and sees broad application for such qualifying terms as edaphic climax and zonal climax, and even for such incongruous sounding phrases as "catena of climaxes." He diagnoses the basic weakness in this whole field by pointing out that "the theory of the climatic climax, indeed the whole structure of ecologic concepts and theories, has been built up on the study of temperate vegetation. . . . It can hardly be doubted that the study of tropical plant communities will greatly modify these concepts and theories, but our knowledge of tropical vegetation is not yet sufficient to justify a full discussion of the theory of climax as applied to rain forest formations." (P. 264.)

Part four (ch. 12-14) is an analysis of sequences and processes in forest successions in tropical regions. The seral systems taken up here are the primary xerosere, under which a good account of the recolonization of Krakatau appears; hydroseres; and the various coastal successions. Although this section leads rather far afield the relevancy of the material to an understanding of the ecologic position of the evergreen rain forest is obvious. The fact that this part is largely comprized by basic descriptive data rather than by theoretical interpretive or correlative considerations again stresses the inadequacy of our comprehension of the processes that produce and maintain rain forest.

Part five (ch. 15-16) is concerned with the rain forest under limiting conditions, as imposed by both altitude and latitude. The biogeographer will find this the most stimulating and suggestive part of the book. It is unfortunate that the gradual replacement, at their latitudinal and altitudinal borders, of the great tropical rain forests of the world is nearly everywhere confused by edaphic variant types or by deflected successional stages. It is difficult, for example, to say just where in Tamaulipas, or in the West Indian arc, the tropical rain forest finds its climatic limits, and this makes it exasperatingly difficult to evaluate the relative importance of geographic and ecologic factors in terminating the northward ranges of tropical animals and plants. The biota of a tropical hammock in South Florida or in the eastern Bahamas has little in common with that of the Trinidad rain forest. To what extent the divergence is due to dispersal factors, and to what extent to ecologic discontinuity, is not apparently known. It is possible to stick a pin in a map to mark the position of the last cloud forest in the Atlantic slope of the Western Hemisphere, but no one ever tries to show exactly where the tropical rain forest, or the "tropical rainforest fauna," gives way. In this section Professor Richards strengthens the grounding for an attack on these questions with his suggestion, which will no doubt shock some plant ecologists, that "there is little support for the view that lowland tropical grasslands are ever a climatic climax in equilibrium with a 'tropical grassland climate'; grassland therefore should not be regarded as occupying a place in the natural climatic ecotone from Tropical Rain forest to desert." (p. 345.)

Part six is called "Man and the Tropical Rain Forest." The single chapter (ch. 17) included here summarizes the scattered published information on secondary and deflected successions in Asia, Africa and Tropical America. Again, important, hitherto unpublished material appears and there is a particularly interesting, though sadly brief, suite of pages on the environmental changes that accompany modified successions. At this point, again, the author finds it necessary to call attention to the elementary development of the field, and he terms the dearth of qualitative and quantitative data on culturally modified rain forest "the most serious gap in our present knowledge" of rain forest ecology.

The text ends with a postscript called "The Future of the Tropical Rain Forest," in which the author emphasizes the accelerating destruction of the world's rain forests, warning that this destruction not only robs us of a resource of immense economic value but wrecks a natural laboratory in which we might have gained "a vast amount of scientific knowledge that could not be obtained elsewhere."

This is a magnificent book and it surely marks the beginning of a new epoch in plant ecology. I only regret Professor Richards' careful avoidance of any transgression of the line setting off the "formation" from the "biome"—the botanical phenomenon from the supercommunity. In other words, I keenly missed a chapter telling what is known, or can be hinted at, or even what is not known, about the basic dynamics of the forest as a whole—about the interplay between the formation and

its animal inhabitants which is the real equilibrium in the climax. I realize that such information is scattered and inadequate, and that Professor Richards' limitation of his scope was conscious and calculated. I still feel that he might have provided us with one more chapter which, if nothing else, would have conveyed an impression of the extreme complexity of this most highly organized of all ecologic communities.

When a biologist walks through a tract of primeval selva and sees a herd of white-lipped peccaries and comes away recalling only pigs in a woods he is seriously missing the point. There can be no doubt that the peccaries, like the beetles and monkeys and ants, are as much a part of the architecture of the forest as its dominant trees, and that any interpretation that does not try to fit them into the scheme is really just a makeshift. The absence of any mention of the role of animals in rain forest ecology in the present book shows how far we are from even a beginning of the laborious process of piecing together the parts of the rain forest ecosystem. It would perhaps be unjust to suggest that the author should have searched out the crumbs of literature on the subject or cluttered his text with the meagre gleanings. I nevertheless feel that somewhere in a work of this stature attention might have been called to the feeble state of this most promising field of inquiry, and to the great gap that exists between the science of forest ecology and an understanding of the rain forest biome type.

But this was not a part of the immense task that Professor Richards set himself, and my comment is no real criticism of this monumental book.

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Social Behavior in Animals[1]

This book, as the author states in his preface, is "characterized by emphasis on the need for renewed and careful observation of the huge variety of social phenomena occurring in nature." By social behavior the author refers to the cooperative responses of individuals to other individuals, and he considers non-social such things as the casual aggregation of certain insects attracted to a lamp.

This small book is packed with interesting information, but the author, an eminent naturalist, makes it clear that it "is not intended as an exhaustive review of facts." His express object has been to present a truly biological approach to the study of social behavior, and furthermore, to present his thoughts in such a way that they can easily be followed by interested non-professionals, in the hope of stimulating research by amateurs.

In his introductory chapter the author gives a brief outline of the life history of three representative species with which he is particularly familiar. These are the herring gull, three-spined stickleback and grayling butterfly. Throughout the book he relies heavily on these three species for illustrations, although he draws examples from many other species as well, particularly among vertebrates. The chapter headings give a good idea of the topics considered: mating behavior, family and group life, fighting, the analysis of social co-operation, relations between different species, the growth of social organization, and the evolutionary aspects of social organization. The discourse is concluded by a chapter, "Some hints for research in animal sociology." The text is illustrated by 67 line drawings and 14 good photographs.

This book is of a less technical nature than the author's well-known book on "The Study of Instinct," although many of the examples are the same, and it likewise lays stress on the importance of social signals and on the innate aspects of behavior. The evidence is presented in a clear and interesting way. At the same time, the need for further experimental verification of many of the conclusions is emphasized by the author. The book is very well organized, replete with stimulating ideas, and the facts are generally supported by citations to the bibliography, which contains 119 references, mostly to European work. There is a four-page index to the names of authors and species mentioned in the text.

There is very little in this able synthesis with which I cannot agree. However, in my opinion, the brief section on "peck-order" (p. 71) is too brief and in some respects, may be misleading. By "peck-order" the author refers to dominance hierarchies based on habitual domination and subordination, and

[1] **Tinbergen, N.** 1953. Social Behaviour in Animals. With special reference to vertebrates. xi + 150 pp., illus. London: Methuen and Co., Ltd.; New York: John Wiley and Sons, Inc. $2.50.

these he considers a minor aspect of social organization. He remarks that "The American literature contains many valuable contributions on the problems of peck-order. In many of these papers, however, peck-order is claimed to be the only principle of social organization. This leads to distorted views; peck-order relationships form only one category among the numerous types of social relationships in existence." One wonders just what references the author has in mind; although he has done a great service by developing in a critical and analytic way many of the other mechanisms of social organization. I have had occasion to review the literature on aggressive dominance several times (Cf. Physiol. Zoöl., 1944, 17: 83-123; Zoologica 1950, 35: 97-119; Annals N. Y. Acad. Sci., 1950., 51: 1074-1092; 1951, Chap. 12 in *Comparative Psychology,* edited by C. P. Stone), and can recall no article by American authors in which "peck-order is claimed to be the only principle of social organization," or even the most important principle of social organization.

The development of a stable dominance order replaces more or less continuous fighting and concomitant excessive punishment by relative tolerance and limited avoidance based on learning, and so is one method of permitting continued aggregation. Many of the American reviews of social behavior, including a number which also deal with social signals, have been concerned to a considerable extent with the origins of sociality and with dominance hierarchies, as special topics of importance for discussion. These reviews, when each is considered in its entirety, have often dealt with the relationship or *balance* between tolerance and aggression. They have uniformly emphasized the dominating role of cooperation, in the sense of mutual benefit, over the socially disruptive aspects of aggression, regardless of the extent to which aggressive behavior depends on innate or learned contributions. This difference in relative emphasis on centripetal as against centrifugal social forces is true not only of the two old references (1931, 1938) to "peck-order" cited by Tinbergen, but also of more than a dozen other reviews published during the subsequent 15 to 20 years, the period in which most of the work on dominance hierarchies has been done.

In the present state of our knowledge the importance of dominance hierarchies in social organization of non-human animals is to some extent a matter of opinion. But much evidence suggests a rather considerable importance, particularly from the viewpoint of the individual, including the apparently widespread occurrence of dominance hierarchies in nature especially among vertebrate animals, and the precedence to food and mates that often goes with high rank in the dominance order. One important function of territorial defense probably is to regulate and prevent excessive despotism in a group of animals by any one member of the group; this function may well be one of the most important reasons why such territorialism has been evolved.

The foregoing remarks, which are largely concerned with differences in emphasis, do not detract from the value of the book. It is a pleasure to recommend it as one that every biologist, indeed every educated person, can read with profit and interest.

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A Synthesis of Paleobiogeography[1]

The authors suggest that this thick volume, developed from a course given at the Faculté des Sciences d'Alger, falls between a textbook and a research memoir. It resembles an historical geology, but unlike most such, not the usual two-theme, alternato-sequential recital of physical and biologic earth history from then till now; it is an attempt to synthesize the interrelated concepts of paleontology, paleoecology, stratigraphy, sedimentology, petrography, tectonics, biology, and ecology, developed around a series of 36 double-page, colored paleobiogeographic-structure world maps which are conveniently assembled between the two main parts of the volume.

The first part, 245 pages of general geology-ecology-sedimentology, includes as principal topics, in order of treatment: basic physical structure of the biosphere, action of the geologic agents, development of basins and geosynclines of deposition, transgressions and regressions, the hydrosphere as the *milieu*

[1] Termier, H. and G. Termier: *Histoire géologique de la biosphère: la vie et les sédiments dans les géographies successives.* Masson, Paris. 1952. 721 p., 8 pls., 117 textfigs., 36 maps, 19 tables. Unbound, 8600 francs; bound, 9200 francs.

vital, illumination and life, topographic distribution of marine organisms, facies and sedimentary cycles, coastal regions as the site of the first organisms, oceanogenic sediments and plankton, role of calcium carbonate and carbon in biology and geology, palaeobiology as the connecting strand of earth history, origin of continents, land bridges, and orogenic "cycles." Further analysis of all these is impractical here and only a few points can be noted.

The two sections on the "general organization of the biosphere, present conditions" and the "conquest and modes of population of the biosphere," pages 66-234, are those of major interest to the ecologist and paleoecologist. The general conditions of existence of aquatic organisms are first sketched, with emphasis on the interrelations of the physical and chemical factors as dissolved gases and salts, and colloids, illumination, temperature, salinity, pH, with an interesting table of the occurrence of the major animal groups in marine, brackish, and fresh waters as they are poecilosmotic or homeosmotic stenohalines or euryhalines. The role of schizophytes, as representatives of the earliest forms of life, and as factors in sedimentation is related to the marine muds as constituting the "soil" of the sea. There follow such topics as biologic associations, facies, adaptation, struggle for existence, succession of biotopes, brief summaries of the ecology and adaptations of the principal groups of marine plants and animals. The last are very unequally treated, and one wonders why the echinoids are given as much space as all other animals put together. In the short chapter on facies and sedimentary cycles, facies (in its stratigraphic sense) is hopelessly confused with the more proper term phase (in its stratigraphic sense). The littoral zone is extensively discussed as a point of departure for the conquest of the brackish and fresh waters on the one hand and of the deeper marine environments on the other. The chapter on the role of calcium carbonate in biology is largely devoted to recent and fossil reefs. The section on fossil reefs or the "history of a facies" (more properly "phase"), is fairly well done, but it is disappointing to see the analysis of fossil reef distribution first presented by the late T. W. Vaughan and the reviewer attributed to Ranson's recent paraphrase.

This entire section represents an attempt to interrelate ecology as understood by most ecologists with sedimentation as understood by most sedimentologists in an outline of paleoecology, a much-needed synthesis, but a very difficult one in which the authors have not succeeded very well. Reading through these badly organized chapters, one has the disconcerting feeling of hopping briskly but erratically from one interesting topic to another rather than moving steadily along a cumulative path of synthesis.

Thus far, the book has aimed at laying a foundation for the consideration of the geologic history of each biotope throughout geologic time, and the demonstration that each has evolved, as announced on page 128. This is a brilliantly conceived idea, here seemingly attempted for the first time, but its promise is scarcely fulfilled. When we turn to this, the second part of the volume, some 386 pages, it has for its title the fairly accurate heading "successive geographies from the pre-Cambrian to our times." The pre-Cambrian, because of its unsolved problems of correlation, masking effects of metamorphism, and paucity of even indirect evidence of organisms, is quickly disposed of in a few pages, with the general conclusion that most, if not all pre-Cambrian sediments were nonmarine. They support Pruvost's recent extension of Menchikoff's Infracambrian as a new system between the pre-Cambrian and the Cambrian, and include here, for instance, the whole of the American Belt series, traditionally placed in the pre-Cambrian by American geologists.

Then come the paleobiogeographic maps. They are based on the Mercator projection, which gives a highly distorted aspect to intercontinental relations across the polar regions. However, this repetition of outmoded cartographic fairy-tales is perhaps outweighed by the clever and telling use of naturalistic symbols for physical phenomena such as sites of volcanism, coarse- and fine-grained sediments, deserts, ice-sheets, old and young mountain ranges, and biologic features such as types of vascular plants, terrestrial animals, ammonites, etc. They are placed where they are authenticated, in spite of what must have been very strong temptation to put them also where they ought to have been. The result has somehow a satisfying effect that makes one wish he could try his hand at it, combining the dynamic physico-biologic symbols of the Termiers with the cartographic skill of a Harrison or a Raisz. Directions of marine migrations are indicated by the customary arrows with a confident hand in many cases quite unwarranted, probably induced in part by the astigmatic effect of our knowledge only of marine transgressions of the continents and general ignorance of the ancient oceans.

The maps are naturally almost wholly compiled from the literature and the list of authorities is imposing. Nevertheless, many errors have crept in, only a few of the more obvious of which can be hinted at here. Contrary to Map 13 (Tournaisian-Early Mis-

sissippian) no goniatite faunas are known in the Pennsylvanian-New York region, nor is there any evidence of a seaway at this time between the central lowland and the Nova Scotia region or Mississippian reefs in the latter place. The next map (No. 14—Viséan) shows goniatites in the New York City region far from any known Mississippian beds. One is surprised to find nothing made of the distribution of *Gigantella*. No late Permian deposits are known in Michigan or Pennsylvania as suggested by Map 18. Coral reefs should have been indicated for the Late Triassic in California and Nevada. It is a jolt to find on Map 21 a dipterid-*Thinnfeldia* flora indicated in the northeastern United States, where no Jurassic rocks are known. Map 26 (Barremian-Aptian) has a coral reef symbol but only one is located on the map, although reefs were fairly widespread at this time in the Tethyan tropical belt. Map 27 (Albian-Cenomanian) doesn't even have a reef symbol, but reefs are known at this time. For the Eocene (Map 31) a little eohippid symbol is shown in the United States, but none in Europe where *Hyracotherium* has long been known. And so on. The last map is organized like those of the earlier epochs but represents the present day. It is well covered with structual and biogeographic symbols in all latitudes and emphasizes the still rudimentary knowledge of paleobiogeography.

From the Cambrian to the Quaternary a few pages are given to the principal epochs of each period, including a chart of broad correlations between the principal terranes, a short biological analysis and paleogeographical survey of each continent.

Pages 650-680 comprise a useful summary bibliography, omitting references easily accessible in standard works such as Suess, Haug, and others, organized more or less according to the order of treatment of topics in the text. About 700 entries indicate the wide, even voracious coverage by the authors. Pages 681-709 carry an index of topics, authors, names of organisms, and geographic and geologic terms, with about 4000 entries.

Illustrations other than the maps include groups of drawings of fossils, placed chronologically in the latter part of the text and intended to illustrate fossil forms "most significant from the biologic and paleogeographic points of view." They are not very well drawn or always well chosen, and add little to the value of the text. Those of many vertebrates verge on the ludicrous. The diagrams serve their purpose better, especially those of the silica, aluminum, sulphur, carbon, iron, and boron cycles. Eight original lithographs by the authors, well-printed on special paper and supposed to give an impression of marine environments and associations of past and present sea coasts, are crude, depressing, and unnecessary embellishments whose omission possibly might have slightly lowered the price of the book.

These last words about price bring us to the book as a technical production. In spite of its high price—about $27 bound and $25 unbound, we may wonder how Masson et Cie had the fortitude to publish it except as a prestige item, for it cannot have a wide sale in spite of its undoubted usefulness. The paper, binding, printing, are excellent and should make American publishers of this type of book look to their somewhat dingy laurels.

The authors, Henrie and Genevieve Termier, the former primarily a physical geologist-petrologist, the latter a paleontologist, constitute a potent husband-wife scientific team, whose voluminous *Paléontologie de Maroc* and numerous short contributions during the past 15 years have led us to expect wide-ranging and often novel things. This time they have not quite brought it off, but they have produced a stimulating book full of ideas, new and old, that should be at the elbow of all aspiring paleoecologists and stratigraphers, and might well cause more ecologists to bring to bear their knowledge of things present on the vast area of things past.

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Plants of Big Bend National Park[1]

As one of our newest (1944) additions, the Big Bend National Part in southwestern Texas is particularly valuable for its unique desert flora shared with neighboring Mexico. The Chisos Mountains, reaching an elevation of 7835 feet, form the heart of the Park and provide an interesting island of encinal and montane associations with some endemic forms. A guide to the rich variety of plant life in this region

[1] **McDougall, W. B., and O. E. Sperry.** 1951. Plants of Big Bend National Park. xi + 209 pp., 191 figs. Washington: Government Printing Office. $1.00.

is, then, especially welcome. Certainly, floras of other national parks have added immeasurably to many tourists' enjoyment.

Introductory pages include a brief sketch of the main vegetative types and explanations of taxonomic terminology with several helpful diagrams of characteristic features. The dichotomous parallel key to the families of vascular plants is based on clear-cut characteristics and statements contrast well. Interestingly written paragraphs describe each family and then each genus, including discussion of the more important species with items of general interest, such as economic use. Excellent photographs illustrate the most characteristic plants and facilitate generic identification.

Species keys are given only with certain genera. For the keener student, usefulness of this booklet would be greatly increased by inclusion of keys for all species. The authors explain that the Cactaceae are only distinguished to genus because species have not been sufficiently studied. However, 43 species have been recognized in the Park and a key for the commoner of these would not be too difficult. The authors acknowledge assistance of specialists in identification of many groups which would indicate a high degree of reliability for the material. However, Fig. 114 seems to be an *Opuntia schottii* mislabelled as *O. pottsii*.

Technical language has been kept to a minimum. Scientific names are preceded by common names wherever possible. Terms which might be new to the reader are well defined in a glossary which is followed by one index for scientific names and another for the common appellations.

The flora of Trans-Pecos Texas is not yet well enough known for a complete, up-to-date manual. Yet some introduction to the plant life is essential groundwork for any research that field biologists undertake in such a changing region. This descriptive key therefore fills a definite need in that respect as well as furnishing a handy and readable guide for any interested visitors to the Park. It is certain to greatly enrich the appreciation of that desert wilderness.

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TABLE OF CONTENTS, VOLUME 34, 1953

Ahlgren, H. L. See Robocker, W. C.

Albertson, F. W., Andrew Riegel, and John L. Launchbaugh, Jr. Effects of different intensities of clipping on short grasses in west-central Kansas 1– 20

Amrein, Yost U. The mode of transmission of non-cyst-forming flagellates in the ovoviviparous yucca night lizard *Xantusia vigilis*..... 243–245

Bank, Theodore P., II. Ecology of prehistoric Aleutian village sites.... 246–264

Barnes, H. On the southern limits of the intertidal barnacle *Balanus balanoides* 429-430

Bartholomew, George A., Jr., William R. Dawson, and Edward J. O'Neill. A field study of temperature regulation in young white pelicans, *Pelecanus erythrorhynchos*..... 554–560

Baylor, Edward R., and Frederick E. Smith. An instrument for quantitative studies of phototaxis..... 224–225

Baylor, Edward R., and Frederick E. Smith. A physiological light trap 223–224

Baylor, E. R. See Grosser, B. I.

Beadle, N. C. W. The edaphic factor in plant ecology with a special note on soil phosphates..... 426–428

Beck, Edwin G. Near extinction of the Celtis petiole gall insect in north Georgia 207

Beenhouwer, Owen. Palynology and the Thornthwaite climatic classification 803–804

Berg, L. S. Are our steppes becoming drier?..... 796–802

Birch, L. C. Experimental background to the study of the distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three grain beetles... 698–711

Birch, L. C. Experimental background to the study of the distribution and abundance of insects. II. The relation between innate capacity for increase in numbers and the abundance of three grain beetles in experimental populations 712-726

Bormann, F. H. The statistical efficiency of sample plot size and shape in forest ecology 474–487

Bourdeau, Philippe F. A test of random versus systematic ecological sampling 499–512

Brayshaw, T. Christopher. See Coupland, Robert T.

Britt, N. Wilson. Differences between measurements of living and preserved aquatic nymphs caused by injury and preservatives..... 802–803

Brown, D. M. Conifer transplants to a grassy bald on Roan Mountain.. 614–617

Buell, Murray F., and John E. Cantlon. Effects of prescribed burning on ground cover in the New Jersey pine region..... 520–528

Burnett, Thomas. Effects of temperature and parasite density on the rate of increase of an insect parasite..... 322–328

Byers, Horace R. Coast redwoods and fog drip..... 192–193

Cantlon, John E. See Buell, Murray F.

CARPENTER, CHARLES C. A study of hibernacula and hibernating associations of snakes and amphibians in Michigan..... 74– 80
CHAPMAN, V. J. See MYERS, E.
CHIASSON, ROBERT B. Fluctuations of some Illinois fox populations.... 617–619
COE, WESLEY R. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents..... 225–229
COLE, GERALD A. Notes on copepod encystment.....208–211
CONSTANCE, LINCOLN. The role of plant ecology in biosystematics..... 642–649
COOKE, WM. BRIDGE. A survey of literature on fungus sociology and ecology—II 211–222
COOPER, HAROLD W. Amounts of big sagebrush in plant communities near Tensleep, Wyoming, as affected by grazing treatment..... 186–189
COOPER, ROBERT, AND EMANUEL D. RUDOLPH. The role of lichens in soil formation and plant succession..... 805–807
COTTAM, GRANT, J. T. CURTIS, AND B. WILDE HALE. Some sampling characteristics of a population of randomly dispersed individuals.... 741–757
COUPLAND, ROBERT T., AND T. CHRISTOPHER BRAYSHAW. The fescue grassland in Saskatchewan.....386–405
CURTIS, J. T. See COTTAM, GRANT.
CURTIS, J. T. See ROBOCKER, W. C.
DAUBENMIRE, R. Nutrient content of leaf litter of trees in the northern Rocky Mountains 786–793
DAVIS, CHARLES C. Concerning the flotation mechanism of Noctiluca.... 189–192
DAWSON, WILLIAM R. See BARTHOLOMEW, GEORGE A., JR.
DAY, GORDON M. The Indian as an ecological factor in the northeastern forest 329–346
DEXTER, RALPH W. Recession of eelgrass at Cape Ann, Massachusetts.. 229–231
EDGREN, MARGERY K. See EDGREN, RICHARD A.
EDGREN, RICHARD A., MARGERY K. EDGREN, AND L. H. TIFFANY. Some North American turtles and their epizoophytic algae 733–740
EGGLER, WILLIS A. The use of 2, 4,-D in the control of water hyacinth and alligator weed in the Mississippi delta, with certain ecological implications 409–414
EGLER, FRANK E. See POUND, CHARLES E.
EMLEN, JOHN T., JR. See STRECKER, ROBERT L.
FERRELL, WILLIAM K. Effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina..... 667–688
FUJITA, HIROSHI, AND SYUNRO UTIDA. The effect of population density on the growth of an animal population..... 488–498
GERKING, SHELBY D. Evidence for the concepts of home range and territory in stream fishes 347–365
GOIN, COLEMAN J., AND OLIVE B. GOIN. Temporal variation in a small community of amphibians and reptiles..... 406–408
GOIN, OLIVE B. See GOIN, COLEMAN J.
GROSSER, B. I., E. R. BAYLOR, AND F. E. SMITH. Analysis of geotactic responses in *Daphnia magna*..... 804–805

HALE, B. WILDE. See COTTAM, GRANT.
HANSON, HERBERT C. Vegetation types in northwestern Alaska and comparisons with communities in other Arctic regions 111–140
HEUSSER, CALVIN J. Radiocarbon dating of the thermal maximum in southeastern Alaska 637–640
HIESEY, WM. M. See JUHREN, MARCELLA.
HIESTAND, WILLIAM A. See STULLKEN, DONALD E.
JACKSON, DANIEL F. *Craspedacusta sowerbii* in Pymatuning Reservoir .. 428–429
JOFFE, J. S. Are our steppes becoming drier? (Berg) 796–802
JUHREN, MARCELLA, WM. M. HIESEY, AND F. W. WENT. Germination and early growth of grasses in controlled conditions 288–300
KEEVER, CATHERINE. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains 44– 54
KHAN, NAWAB H. Effects of weather conditions on horsefly populations 414–415
KÜCHLER, A. W. Some uses of vegetation maps 629–636
KURIYAN, G. K. Biology of fouling in the Gulf of Manaar: a preliminary account 689–692
KURZ, HERMAN, AND KENNETH A. WAGNER. Factors in cypress dome development 157–164
LAUNCHBAUGH, JOHN L., JR. See ALBERTSON, F. W.
LEISMAN, GILBERT A. The rate of organic matter accumulation on the sedge mat zones of bogs in the Itasca State Park region of Minnesota 81–101
LINDROTH, CARL H. Some attempts toward experimental zoogeography .. 657–666
LINDSAY, DOUGLAS R. Climate as a factor influencing the mass ranges of weeds 308–321
MARSHALL, NELSON. The balanoid biome-type of intertidal rocky shores 434–436
MARTOF, BERNARD. Home range and movements of the green frog, *Rana clamitans* 529–543
MARTOF, BERNARD. Territoriality in the green frog, *Rana clamitans* 165–174
MARTOF, BERNARD. The "spring lizard" industry: a factor in salamander distribution and genetics 436–437
MCMILLAN, JOHN F. Some feeding habits of moose in Yellowstone Park 102–110
MIDDLETON, W. E. KNOWLES. Spherical illumination as an ecological parameter, and an improved integrator 416–421
MYERS, E., AND V. J. CHAPMAN. Statistical analysis applied to a vegetation type in New Zealand 175–185
NEEDHAM, JAMES G. Archbold Biological Station 649
NIELSEN, ASTRID TETENS. See NIELSEN, ERIK TETENS.
NIELSEN, ERIK TETENS, AND ASTRID TETENS NIELSEN. Field observations on the habits of *Aedes taeniorhynchus* 141–156
NORRIS, KENNETH S. The ecology of the desert iguana *Dipsosaurus dorsalis* 265–287
OLIVE, JOHN R. The occurrence of the cladoceran *Leptodora kindtii* in Colorado 628–629
O'NEILL, EDWARD J. See BARTHOLOMEW, GEORGE A., JR.
ORGAIN, HOLMES, AND MARTIN W. SCHEIN. A preliminary analysis of the physical environment of the Norway rat 467–473

PARKER, JOHNSON. Photosynthesis of *Picea excelsa* in winter..... 605–609
PARMALEE, PAUL W. Food and cover relationships of the bobwhite quail in east-central Texas..... 758–770
PAULSEN, HAROLD A., JR. A comparison of surface soil properties under mesquite and perennial grass..... 727–732
PEARSON, PAUL G. A field study of *Peromyscus* populations in Gulf Hammock, Florida..... 199–207
PELTON, JOHN. Ecological life cycle of seed plants..... 619–628
PENFOUND, WM. T. Plant communities of Oklahoma lakes..... 561–583
PETERSEN, ROALD A. Comparative effect of seed treatments upon seedling emergence in seven browse species..... 778–785
POUND, CHARLES E., AND FRANK E. EGLER. Brush control in southeastern New York: fifteen years of stable tree-less communities.... 63– 73
RANDALL, WILLIAM E., JR. Water relations and chlorophyll content of forest herbs in southern Wisconsin..... 544–553
RAUSCH, ROBERT. Studies on the helminth fauna of Alaska. XIII. Disease in the sea otter, with special reference to helminth parasites.... 584–604
RIEGEL, ANDREW. See ALBERTSON, F. W.
ROBOCKER, W. C., J. T. CURTIS, AND H. L. AHLGREN. Some factors affecting emergence and establishment of native grass seedlings in Wisconsin..... 194–199
RUDOLPH, EMANUEL D. See COOPER, ROBERT.
RUSSELL, NORMAN H. The beech gaps of the Great Smoky Mountains.. 366–374
SCHEIN, MARTIN W. See ORGAIN, HOLMES.
SHANKS, ROYAL E. Forest composition and species association in the beech-maple forest region of western Ohio..... 455–466
SHARP, WARD M. A reevaluation of plant communities within the pheasant range in the Nebraska sandhills..... 771–777
SHELFORD, V. E. An experimental approach to the study of plant and animal reproductivity and population with a life science building plan.. 422–426
SLOBODKIN, L. BASIL. An algebra of population growth..... 513–519
SLOBODKIN, L. BASIL. On social single species populations..... 430–434
SMITH, FREDERICK E. See BAYLOR, EDWARD R.
SMITH, FREDERICK E. See GROSSER, B. I.
SMITH, OSGOOD R. Notes on the ability of the horseshoe crab, *Limulus polyphemus,* to locate soft-shell clams, *Mya arenaria*..... 636–637
SMITH, OSGOOD R. Observations on the rate of decay of soft-shell clams (*Mya arenaria*)..... 640–641
STANLEY, JOHN. Studies from the autotrephon, I. Some points in general operation and maintenance..... 21– 28
STANLEY, JOHN. Studies from the autotrephon, II. The analysis of autotrephon data..... 29– 43
STRECKER, ROBERT L., AND JOHN T. EMLEN, JR. Regulatory mechanisms in house-mouse populations: the effect of limited food supply on a confined population..... 375–385
STULLKEN, DONALD E., AND WILLIAM A. HIESTAND. An experimental study of the influence of pelage pigmentation on metabolic rate and

its possible relationship to body temperature control and ecological distribution 610–613
SUTCLIFFE, W. H., JR. Notes on the biology of a spiny lobster, *Panulirus guttatus*, in Bermuda 794-796
TIFFANY, L. H. See EDGREN, RICHARD A.
TURNER, HARRY J., JR. The drilling mechanism of the Naticidae 222–223
UTIDA, SYUNRO. Interspecific competition between two species of bean weevil 301–307
UTIDA, SYUNRO. See FUJITA, HIROSHI.
VERNBERG, F. JOHN. Hibernation studies of two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata* 55– 62
WAGNER, KENNETH A. See KURZ, HERMAN.
WARBURTON, FREDERICK E. Antagonism between different species of hydroids on the same shell 193–194
WENT, F. W. See JUHREN, MARCELLA.
WILSON, CHARLES C. The rate of apparent photosynthesis of some broad-leaf evergreens 693–697
Reviews, 232, 233, 236, 237, 238, 438, 440, 442, 443, 446, 447, 449, 450, 451, 650, 651, 654, 655, 808, 810, 811, 813
Book Notices 240
Books Received for Review 452, 655, 814
Announcement 453
Index to Volume 34 823

INDEX TO VOLUME 34, 1953

A

Abundance of grain beetles, 712
Accumulation, rate of organic matter on the sedge mat zones of bogs in the Itasca State Park region of Minnesota, article, 81-101
Activity, seasonal, of green frog, 529
Acdes taeniorhynchus, mosquito, habits of, 141
Ahlgren, H. L., co-author, note, 194-199
Alaska, helminth parasites of sea otter of, 584
Alaska, northwestern, vegetation types in and comparisons with communities in other Arctic regions, article, 111-140
Alaska, southeastern, radiocarbon dating of the thermal maximum in, note, 637-640
Albertson, F. W., Andrew Riegel, and John L. Launchbaugh, Jr., article, 1-20
Aleutian village sites, prehistoric, ecology of, article, 246-264
Algae, epizoophytic, on turtles, 733
Algebra of population growth, article, 513-519
Allen, A. A., review, 451
Ambloplites rupestris, rock bass, home range of, 347
Amounts of big sagebrush in plant communities near Tensleep, Wyoming, as affected by grazing treatment, note, 186-189
Amphibians, hibernation of, 55, 74
Amphibians in Florida, 406
Amrein, Yost U., article, 243-245
Analysis of geotactic responses in *Daphnia magna,* note, 804-805
Analysis, statistical, applied to a vegetation type in New Zealand, article, 175-185
Animal population, growth affected by density, 488
An instrument for quantitative studies of phototaxis, note, 224-225
Antagonism between different species of hydroids on the same shell, note, 193-194
Anthony, Margery S., review, 813-814
Appalachians, southern, salamanders in, 436
Archbold Biological Station, note, 649
Archey, Gilbert, reviewed, 236
Arctic, vegetation types in northwestern Alaska and comparisons with communities in other regions, article, 111-140
Are our steppes becoming drier? (Berg), note, 796-802
Attachment of fouling organisms, 689
Autotrephon, data analysis, 29
Autotrephon, operation and maintenance, 21

B

Balanoid biome-type of intertidal rocky shores, note, 434-436
Balanus balanoides, barnacle, southern limits of, 429
Balanus spp., as fouling organisms, 689
Bald, grassy, conifer transplants to, on Roan Mountain, note, 614-617
Baltimore, Norway rats in, 467
Bank, Theodore P., II, article, 246-264
Barnacle, *Balanus balanoides,* southern limits of, 429
Barnes, H., note, 429-430
Bartholomew, George A., Jr., William R. Dawson, and Edward J. O'Neill, article, 554-560
Basicladia spp., algae, on turtles, 733
Bass, home range of, 347
Bates, Marston, reviewed, 447-449
Baxter, Dow Vawter, book notice, 240
Baylor, Edward R., and Frederick E. Smith, note, 223-224; 224-225
Baylor, E. R., co-author, note, 804-805
Beadle, N. C. W., note, 426-428
Bean weevils, competition in, 301
Beck, Edwin G., note, 207
Beech gaps of the Great Smoky Mountains, article, 366-374
Beenhouwer, Owen, note, 803-804
Beetles, carabid, zoogeography of, 657
Beginning of a new era in Mexican ornithology (Blake), review, 654
Berg, L. S., note, 796-802
Bermuda, notes on biology of spiny lobster in, 794
Bertalanffian organismicism, review, 443-446
Bertalanffy, Ludwig von, reviewed, 443-446
Biological investigations in Mexico, reviewed, 446-447
Biology of fouling in the Gulf of Manaar: a preliminary account, article, 689-692
Biology of Paramecium (Wichterman), review, 651-654
Biology of spiny lobster, notes on, 794
Biosystematics, role of plant ecology in, note, 642-649
Biotic world and man, book notice, 240
Birch, L. C., article, 698-711
Birch, L. C., article, 712-726
Birds of Mexico, a guide for field identification, reviewed, 654
Blake, Emmet Reid, reviewed, 654
Blue Ridge, present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains, article, 44-54
Bobwhite quail, in east-central Texas, 758
Bogs, rate of organic matter accumulation on the sedge mat zones of, in the Itasca State Park region of Minnesota, article, 81-101
Bormann, F. H., article, 474-487
Bourdeau, Philippe F., article, 409-512
Boyce, J. S., book notice, 240
Brayshaw, T. Christopher, co-author, article, 386-405
Britt, N. Wilson, note, 802-803
Broadleaf evergreens, the rate of apparent photosynthesis of some, article, 693-697

Brown, D. M., note, 614-617
Browse species, comparative effect of seed treatments upon seedling emergence in seven, article, 778-785
Browsing by moose, 102
Brush control in southeastern New York: fifteen years of stable tree-less communities, article, 63-73
Buell, Murray F., and John E. Cantlon, article, 520-528
Burbanck, W. D., review, 651-654
Burnett, Thomas, article, 322-328
Burning, prescribed, effects of, on ground cover in the New Jersey pine region, article, 520-528
Burrows of desert iguana, 265
Burt, W. H., and R. P. Grossenheider, reviewed, 449-450
Byers, Horace R., note, 192-193

C

Calandra oryzae, grain beetle, innate capacity for increase of, affected by food, temperature, and moisture, 698
California, barnacles of, 430
Callosobruchus spp., bean weevils, competition between, 301
Cantlon, John E., co-author, article, 520-528
Cape Ann, Massachusetts, eelgrass at, 229
Carabid beetles of Fennoscandia, 657
Carbon dioxide fixation and photosynthesis, review, 238-239
Carpenter, Charles C., article, 74-80
Carr, Archie, review, 808-810
Celtis petiole gall insect in north Georgia, near extinction of the, note, 207
Chapman, V. J., co-author, article, 175-185
Chemical factors in substrate, affecting beetles, 657
Chiasson, Robert B., note, 617-619
Chlorophyll content, water relations and, of forest herbs in southern Wisconsin, article, 544-553
City rat population, physical environment of, 467
Cladocera, light trap for, 223
Cladoceran, *Daphnia magna,* geotactic responses in, 804
Cladoceran, *Leptodora kindtii,* in Colorado, 628
Clam, soft-shell, located by horseshoe crab, 636
Clam, soft-shell, rate of decay of, 640
Classification, the Thornthwaite climatic, palynology and, note, 803-804
Clausen, Jens, reviewed, 233-235
Clay, Teresa, co-author, book notice, 240
Climate as a factor influencing the mass ranges of weeds, article, 308-321
Climatic classification, Thornthwaite, palynology and the, note, 803-804
Clipping, effects of different intensities of, on short grasses in west-central Kansas, article, 1-20
Coast redwoods and fog drip, note, 192-193
Coe, Wesley R., note, 225-229
Cole, Gerald A., note, 208-211
Colinus virginianus, bobwhite quail, in east-central Texas, 758
Collias, N. E., review, 810-811
Colorado, *Leptodora kindtii,* cladoceran, in, 628
Commensalism between turtles and algae, 733
Communities, plant, of Oklahoma lakes, article, 561-583
Comparative effect of seed treatments upon seedling emergence in seven browse species, article, 778-785
Comparison of surface soil properties under mesquite and perennial grass, article, 727-732
Competition in bean weevils, 301
Composition, present, of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains, article, 44-54
Concerning the flotation mechanism of *Noctiluca,* note, 189-192
Conifer transplants to a grassy bald on Roan Mountain, note, 614-617
Constance, Lincoln, note, 642-649
Control, brush, in southeastern New York: fifteen years of stable tree-less communities, article, 63-73
Control of water hyacinth and alligator weed in the Mississippi delta, use of 2,4,-D in the, with certain ecological implications, note, 409-414
Controlled conditions, germination and early growth of grasses in, article, 288-300
Cooke, Wm. Bridge, note, 211-222
Cooper, Harold W., note, 186-189
Cooper, Robert, note, 805-807
Copepod encystment, 208
Corynosoma strumosum, acanthocephalan, in sea otter, 584
Cottam, Grant, article, 741-757
Coupland, Robert T., and T. Christopher Brayshaw, article, 386-405
Cover and food relationships of quail, 758
Craspedacusta sowerbii in Pymatuning Reservoir, note, 428-429
Currents, ocean and tidal, affecting littoral invertebrates, 225
Curtis, J. T., co-author, note, 194-199
Curtis, J. T., co-author, article, 741-757
Cypress dome development, factors in, article, 157-164

D

Dahlbominus fuscipennis, parasitic insect, populations of, 322
Dansereau, Pierre, reviews, 232-233; 233-235; 447-449
Daphnia magna, geotactic responses in, 804
Dating, radiocarbon, of the thermal maximum in southeastern Alaska, note, 637-640
Daubenmire, R., article, 786-793
Davis, Charles C., note, 189-192
Dawson, William R., co-author, article, 554-560

Day, Gordon M., article, 329-346
Decay of soft-shell clam, 640
Deevey, E. S., book notices, 240, 241
Density of population, affecting population increase, 322, 712
Density of population, effect of, on growth of an animal population, 488
Desert bird, white pelican, temperature regulation in young of, 554
Desert iguana, ecology of, 265
Desert lizard, *Xantusia vigilis*, transmission of flagellates in, 243
Dexter, Ralph W., note, 229-231
Dexter, Ralph W., review, 438-440
Dice, L. R., reviewed, 438-442
Diet of moose, 102
Differences between measurements of living and preserved aquatic nymphs caused by injury and preservatives, note, 802-803
Dimorphism, wing, in carabid beetles, 657
Donax spp., bivalve mollusks, population fluctuations in, 225
Drilling mechanism of the Naticidae, note, 222-223
Drip, fog, coast redwoods and, note, 192-193

E

Early growth, germination and, of grasses in controlled conditions, article, 288-300
Ecological distribution, relation of to pelage pigmentation, 610
Ecological life cycle of seed plants, note, 619-628
Ecological parameter, spherical illumination as an, and an improved integrator, note, 416-421
Ecology, fungus sociology and—II, survey of literature on, note, 211-222
Ecology of prehistoric Aleutian village sites, article, 246-264
Ecology of sessile marine organisms, review, 442-443
Ecology of the desert iguana *Dipsosaurus dorsalis*, article, 265-287
Edaphic factor in plant ecology with a special note on soil phosphates, note, 426-428
Edgren, Margery K., co-author, article, 733-740
Edgren, Richard A., Margery K. Edgren, and L. H. Tiffany, article, 733-740
Eelgrass, recession of, 229
Effect, comparative, of seed treatments upon seedling emergence in seven browse species, article, 778-785
Effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina, article, 667-688
Effect of population density on the growth of an animal population, article, 488-498
Effects of different intensities of clipping on short grasses in west-central Kansas, article, 1-20
Effects of prescribed burning on ground cover in the New Jersey pine region, article, 520-528
Effects of temperature and parasite density on the rate of increase of an insect parasite, article, 322-328
Effects of weather conditions on horsefly populations, note, 414-415
Efficiency, statistical, of sample plot size and shape in forest ecology, article, 474-487
Eggler, Willis A., note, 409-414
Egler, Frank E., co-author, article, 63-73
Egler, Frank E., review, 443-446
Eighth International Congress of Botany, announcement, 453
Emergence and establishment of native grass seedlings in Wisconsin, some factors affecting, note, 194-199
Emlen, John T., co-author, article, 375-385
Encystment of copepods, 208
Enhydra lutris, sea otter, helminth parasites of, 584
Environment, physical, of Norway rat, 467
Environmental conditions, effect of on survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina, article, 667-688
Ephemera simulans, mayfly, measurements of, 802
Epizoophytic algae, on turtles, 733
Esquema ecologico de selva, sabana y cordillera en Bolivia, reviewed, 232-233
Establishment of native grass seedlings in Wisconsin, some factors affecting emergence and, note, 194-199
Eurycea bislineata bislineata, salamander, hibernation studies of, 55
Evidence for the concepts of home range and territory in stream fishes, article, 347-365
Experimental approach to the study of plant and animal reproductivity and population with a life science building plan, note, 422-426
Experimental background to the study of the distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three grain beetles, article, 698-711
Experimental background to the study of the distribution and abundance of insects. II. The relation between innate capacity for increase in numbers and the abundance of three grain beetles in experimental populations, article, 712-726
Experimental study of the influence of pelage pigmentation on metabolic rate and its possible relationship to body temperature control and ecological distribution, article, 610-613
Extinction, near, of the Celtis petiole gall insect in north Georgia, note, 207

F

Factors affecting emergence and establishment of native grass seedlings in Wisconsin, note, 194-199
Factors in cypress dome development, article, 157-164
Feeding habits of moose, 102
Fennoscandia, zoogeography of beetles of, 657
Fenton, Frederick A., reviewed, 237
Ferrell, William K., article, 667-688
Fescue grassland in Saskatchewan, article, 386-405
Field crop insects, review, 237
Field guide to the mammals, review, 449-450
Field observations of the habits of *Aedes taeniorhynchus,* article, 141-156
Field study of Peromyscus populations in Gulf Hammock, Florida, note, 199-207
Field study of temperature regulation in young white pelicans, *Pelecanus erythrorhynchos,* article, 554-560
Fish, home range and territory in, 347
Flagellates in yucca night lizard, 243
Fleas, flukes, and cuckoos. A study of bird parasites, book notice, 240
Florida, amphibians and reptiles in, 406
Florida, habits of *Aedes taeniorhynchus* in, 141
Florida, *Peromyscus* populations in, 199
Flotation mechanism of *Noctiluca,* 189
Flour beetle, *Tribolium confusum,* in autotrephon, 29
Fluctuations in some Illinois fox populations, note, 617-619
Fog drip, coast redwoods and, note, 192-193
Food, affecting increase of grain beetles, 698
Food and cover relationships of the bobwhite quail in east-central Texas, article, 758-770
Food supply, limited, affecting house-mouse populations, 375
Food supply of urban rats, 467
Forest ecology, statistical efficiency of sample plot size and shape in, article, 474-487
Forest entomology, review, 237-238
Forest herbs in southern Wisconsin, water relations and chlorophyll content of, article, 544-553
Forest, northeastern, the Indian as an ecological factor in the, article, 329-346
Forest, oak-chestnut, present composition of some stands of the former, in the southern Blue Ridge Mountains, article, 44-54
Forest tree seedlings, effect of environmental conditions on survival and growth of, under field conditions in the Piedmont region of North Carolina, article, 667-688
Fouling, biology of, 689
Fox populations, fluctuations in, 617
Friend, Roger B., review, 237-238
Frog, *Rana clamitans,* home range and movements of, 529
Frog, *Rana clamitans,* territoriality in, 165
Fujita, Hiroshi, and Syunro Utida, article, 488-498
Fungus sociology and ecology—II, survey of literature on, note, 211-222

G

Galston, Arthur W., review, 238-239
General genetics, review, 450-451
Georgia, north, near extinction of the Celtis petiole gall insect in, note, 207
Geotactic responses in *Daphnia magna,* 804
Gerking, Shelby D., article, 347-365
Germination and early growth of grasses in controlled conditions, article, 288-300
Goin, Coleman J., and Olive B. Goin, note, 406-408
Goldman, Edward Alphonso, reviewed, 446-447
Graham, Samuel Alexander, reviewed, 237-238
Grain beetles, population study of, 698, 712
Grass, mesquite and perennial, a comparison of surface soil properties under, article, 727-732
Grass seedlings, native, some factors affecting emergence and establishment of, in Wisconsin, note, 194-199
Grasses, germination and early growth of, in controlled conditions, article, 288-300
Grasses, short, effects of different intensities of clipping on in west-central Kansas, article, 1-20
Grassland, fescue, in Saskatchewan, article, 386-405
Grazing treatment, amounts of big sagebrush in plant communities near Tensleep, Wyoming, as affected by, note, 186-189
Great Smoky Mountains, beech gaps of the, article, 366-374
Grossenheider, R. P., co-author, reviewed, 449-450
Grosser, B. I., E. R. Baylor, and F. E. Smith, note, 804-805
Ground cover in the New Jersey pine region, effects of prescribed burning on, article, 520-528
Growth, early, germination and, of grasses in controlled conditions, article, 288-300
Growth, survival and, of forest tree seedlings under field conditions in the Piedmont region of North Carolina, effect of environmental conditions on, article, 667-688
Guide for field identification, reviewed, 654
Gulf Hammock, Florida, mouse populations in, 199
Gulf of Manaar, fouling organisms in, 689

H

Habitat of desert iguana, 265
Habitat of green frog, 529
Hale, B. Wilde, co-author, article, 741-757
Hanson, Herbert C., article, 111-140
Helminth parasites of sea otter, 584

Herbs, forest, water relations and chlorophyll content of, in southern Wisconsin, article, 544-553
Heusser, Calvin J., note, 637-640
Hibernation in desert iguana, 265
Hibernation of green frog, 529
Hibernation of snakes and amphibians, 74
Hibernation studies of two species of salamanders, *Plethodon cinereus cinerus* and *Eurycea bislineata bislineata*, article, 55-62
Hiesey, Wm. M., co-author, article, 288-300
Hiestand, William A., co-author, article, 610-613
Histoire géologique de la biosphère: la vie et les sédiments dans les géographies successives, reviewed, 811-813
Home range and movements of the green frog, *Rana clamitans*, article, 529-543
Home range in stream fishes, 347
Horsefly populations, effect of weather on, 414
Horseshoe crab, *Limulus polyphemus*, ability of to locate soft-shell clams, 636
House-mouse populations, regulatory mechanisms in, 375
Humidity, affecting desert iguana, 265
Hydractinia echinata, hydroid, habit of, 193
Hydroids, antagonism between species of, 193
Hyman, Libbie Henrietta, book notice, 241
Hypentelium nigricans, sucker, home range of, 347

I

Idiopathic enteritis of sea otter, 584
Iguana, *Dipsosaurus dorsalis*, ecology of, 265
Illinois, fluctuation of fox populations in, 617
Illumination, spherical, as an ecological parameter, and an improved integrator, note, 416-421
Immaculate forest (Philipson), review, 655
Increase in number of grain beetles, 698, 712
Indian as an ecological factor in the northeastern forest, article, 329-346
Indiana, territoriality of stream fishes in, 347
Insect nymphs, aquatic, measurement of, 802
Integration of the ecospecies, review, 233-235
Integrator, spherical illumination as an ecological parameter, and an improved integrator, note, 416-421
Intemperate man in the tropics (Bates), review, 447-449
Interspecific competition between two species of bean weevil, article, 301-307
Invertebrate zoology with paleontological emphasis (Shrock and Twenhofel), review, 650-651
Invertebrates, littoral marine, and currents, 225
Invertebrates: Platyhelminthes and Rhynchocoela, the acoelomate Bilateria; Acanthocephala, Aschelminthes, and Entoprocta, the pseudocoelomate Bilateria, book notice, 241
Itasca State Park region of Minnesota, rate of organic matter accumulation on the sedge mat zones of bogs in, article, 81-101

J

Jackson, Daniel F., note, 428-429
Joffe, J. S., note, 796-802
Juhren, Marcella, Wm. M. Hiesey, and F. W. Went, article, 288-300

K

Kansas, west-central, effects of different intensities of clipping on short grasses, article, 1-20
Keever, Catherine, article, 44-54
Kendeigh, S. C., reviewed, 451
Khan, Nawab H., note, 414-415
Kring, James B., review, 237
Küchler, A. W., note, 629-636
Kuriyan, G. K., article, 689-692
Kurz, Herman, and Kenneth A. Wagner, article, 157-164

L

Lakes, Oklahoma, plant communities of, article, 561-583
Launchbaugh, John L., Jr., co-author, article, 1-20
Leaf litter of trees in the northern Rocky Mountains, nutrient content of, article, 786-793
Leisman, Gilbert A., article, 81-101
Lepomis spp., sunfish, home range of, 347
Leptodora kindtii, cladoceran, in Colorado, 628
Lichens, the role of, in soil formation and plant succession, note, 805-807
Life cycle, ecological, of seed plants, note, 619-628
Life science building plan, 422
Life table for grain beetle, 698
Limulus polyphemus, horseshoe crab, ability of to locate soft-shell clams, 636
Lindroth, Carl H., article, 657-666
Lindsay, Douglas R., article, 308-321
Literature, survey of, on fungus sociology and ecology—II, note, 211-222
Litter, leaf, nutrient content of, of trees in the northern Rocky Mountains, article, 786-793
Little, Thomas M., review, 450-451
Lizard, *Xantusia vigilis*, transmission of flagellates in, 243
Lobster, spiny, notes on biology of, 794
Lytocarpus, hydroid, as a fouling organism, 689

M

Maguire, B., Jr., review, 655
Mann, Guillermo, reviewed, 232-233
Maps, vegetation, some uses of, note, 629-636
Marine fouling and its prevention, reviewed, 442-443
Marine invertebrates, dependent upon currents, 225
Marshall, Nelson, note, 434-436
Martof, Bernard, article, 529-543
Martof, Bernard, article, 165-174

Mass ranges of weeds, climate as a factor influencing the, article, 308-321
Massachusetts, eelgrass in, 229
Mayfly nymphs, measurements of, 802
McDougall, W. B., and O. E. Sperry, reviewed, 813-814
McMillan, John F., article, 102-110
Measurements of living and preserved aquatic nymphs, differences between, 802
Mesquite and perennial grass, a comparison of surface soil properties under, article, 727-732
Metabolic rate, influence of pelage pigmentation upon, 610
Methodology and the community concept, review, 440-442
Michigan, hibernation of snakes and amphibians in, 74
Michigan, home range of green frog of, 529
Microphallus pirum, trematode, in sea otter, 584
Micropterus spp., bass, home range of, 347
Middleton, W. E. Knowles, note, 416-421
Milne, Lorus J., and M. J. Milne, book notice, 240
Minnesota, Itasca State Park region of, rate of organic matter accumulation on the sedge mat zones of bogs, article, 81-101
Mississippi delta, use of 2, 4,-D in the control of water hyacinth and alligator weed in the, with certain ecological implications, note, 409-414
Mode of transmission of non-cyst-forming flagellates in the ovoviviparous yucca night lizard *Xantusia vigilis,* article, 243-245
Moisture, affecting increase of grain beetles, 698
Mulluscs, drilled by Naticidae, 222
Monocercomonas colubrorum, intestinal flagellate, in a lizard, 243
Monocercomonoides lacertae, intestinal flagellate, in a lizard, 243
Moose, feeding habits, 102
Mortality of soft-shell clam, 640
Mosquito habits, 141
Mouse populations, regulatory mechanisms in, 375
Moxostoma erythrurum, golden redhorse, home range of, 347
Murie, Olaus J., review, 236
Mus musculus, house-mouse, regulatory mechanisms in populations of, 375
Mya arenaria, soft-shell clam, located by horseshoe crab, 636
Mya arenaria, soft-shell clam, rate of decay of, 640
Myers, E., and V. J. Chapman, article, 175-185

N

Naticidae, drilling mechanism of, 222
Natural communities, reviewed, 438-442
Near extinction of the Celtis petiole gall insect in north Georgia, note, 207
Nebraska sandhills, a reevaluation of plant communities within the pheasant range in the, article, 771-777
Needham, James G., note, 649
Neodiprion sertifer, sawfly, host to a parasite, 322
New Jersey pine region, effects of prescribed burning on ground cover in the, article, 520-528
New York, brush control in southeastern: fifteen years of stable tree-less communities, article, 63-73
New Zealand, statistical analysis applied to a vegetation type in, article, 175-185
Nielsen, Erik Tetens, and Astrid Tetens Nielsen, article, 141-156
Noctiluca miliaris, flotation mechanism of, 189
Norris, Kenneth S., article, 265-287
North Carolina, the Piedmont region of, effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in, article, 667-688
Northeastern forest, the Indian as an ecological factor in the, article, 329-346
Notes on copepod encystment, note, 208-211
Notes on the ability of the horseshoe crab, *Limulus polyphemus,* to locate soft-shell clams, *Mya arenaria,* note, 636-637
Notes on the biology of a spiny lobster, *Panulirus guttatus,* in Bermuda, note, 794-796
Nutrient content of leaf litter of trees in the northern Rocky Mountains, article, 786-793

O

Oak-chestnut, present composition of some stands of the former forest in the southern Blue Ridge Mountains, article, 44-54
Observations on the rate of decay of soft-shell clams (*Mya arenaria*), 640-641
Occurrence of the cladoceran *Leptodora kindtii* in Colorado, note, 628-629
Ocean currents, effect on littoral invertebrates, 225
Oklahoma lakes, plant communities of, article, 561-583
Olive, John R., note, 628-629
O'Neill, Edward J., co-author, article, 554-560
On social single species populations, note, 430-434
On the southern limits of the intertidal barnacle *Balanus balanoides,* note, 429-430
Orgain, Holmes, and Martin W. Schein, article, 467-473
Organic matter, rate of accumulation on the sedge mat zones of bogs in the Itasca State Park region of Minnesota, article, 81-101
Orthosplanchus fraterculus, trematode, in sea otter, 584
Ostrea cucullata, rock oyster, as a fouling organism, 689
Owen, Ray D., co-author, reviewed, 450-451

P

Palynology and the Thornthwaite climatic classification, note, 803-804
Panulirus guttatus, spiny lobster, notes on biology of, 794
Parasites, helminth, of sea otter, 584
Parasitic insect, population increase of, 322
Parasitism and interspecific competition, 301
Parental care and its evolution in birds, review, 451
Park, Orlando, review, 440-442
Parker, Johnson, article, 605-609
Parmalee, Paul W., article, 758-770
Pathology in forest practice, book notice, 240
Paulsen, Harold A., Jr., article, 727-732
Paynter, Raymond A., Jr., review, 654
Pearson, Paul G., note, 199-207
Pelage pigmentation and temperature control, 610
Pelican, *Pelecanus erythrorhynchos,* temperature regulation in, 554
Pelton, John, note, 619-628
Penfound, Wm. T., article, 561-583
Pennaria disticha, hydroid, as a fouling organism, 689
Peromyscus spp., populations in Florida, 199
Peterson, Roald A., article, 778-785
Petiole gall insect, of Celtis, near extinction of in north Georgia, note, 207
Pheasant range in the Nebraska sandhills, a reevaluation of plant communities within the, article, 771-777
Philipson, W. R., reviewed, 655
Phocitrema fusiforme, trematode, in sea otter, 584
Phosphates, soil, the edaphic factor in plant ecology with a special note on, note, 426-428
Photosynthesis, apparent, of some broadleaf evergreens, the rate of, article, 693-697
Photosynthesis of *Picea excelsa* in winter, article, 605-609
Phototaxis, instrument for study of, 224
Physical environment of Norway rat, 467
Physiological light trap, note, 223-224
Picea excelsa, phytosynthesis of in winter, article, 605-609
Piedmont region of North Carolina, effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the, article, 667-688
Pigmentation of pelage and temperature control, 610
Pine region, New Jersey, effects of prescribed burning on ground cover in the, article, 520-528
Pioneer effort in Mexican biogeography (Goldman), review, 446-447
Pitelka, Frank A., review, 446-447
Plant communities, a reevaluation of, within the pheasant range in the Nebraska sandhills, article, 771-777
Plant communities near Tensleep, Wyoming, amounts of big sagebrush in, as affected by grazing treatment, note, 186-189
Plant communities of Oklahoma lakes, article, 561-583
Plant ecology, role of in biosystematics, note, 642-649
Plants of Big Bend National Park (McDougall & Sperry), review, 813-814
Plethodon c. cinereus, salamander, hibernation studies of, 55
Plot, sample, statistical efficiency of size and shape in forest ecology, article, 474-487
Podocoryne carnea, hydroid, habit of, 193
Polynices duplicata, snail, boring mechanism of, 222
Polyzoa, as fouling organisms, 689
Population density, effect of on growth of an animal population, 488
Population growth, algebra of, 513
Population increase of an insect parasite, 322
Population of Norway rats, physical environment of, 467
Population of randomly dispersed individuals, some sampling characteristics of a, article, 741-757
Population studies of grain beetles, 698, 712
Population theory, 430
Populations, house-mouse, regulatory mechanisms, 375
Populations of bean weevils, competition between, 301
Populations of marine invertebrates, dependence on currents, 225
Populations of *Peromyscus* spp. in Florida, 199
Porrocaecum decipiens, nematode, in sea otter, 584
Post oak region of Texas, food and cover of quail in, 758
Pound, Charles E. and Frank E. Egler, article, 63-73
Prehistoric Aleutian village sites, ecology of, article, 246-264
Preliminary analysis of the physical environment of the Norway rat, article, 467-473
Prescribed burning, effects of, on ground cover in the New Jersey pine region, article, 520-528
Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains, article, 44-54
Preservatives, effect of, on measurements of aquatic nymphs, 802
Pricetrema zalophi, trematode, in sea otter, 584
Principles of community ecology, review, 438-440
Principles of invertebrate paleontology, reviewed, 650-651
Problems of life, an evaluation of modern biological thought, reviewed, 443-446
Pyramicocephalus phocarum, cestode, in sea otter, 584

Q

Quail, in east-central Texas, 758

R

Radiocarbon dating of the thermal maximum in southeastern Alaska, note, 637-640
Rainforest, savana, and high mountain in Bolivia (Mann), review, 232-233
Rana clamitans, green frog, home range and movements of, 529
Rana clamitans, green frog, territoriality in, 164
Randall, William E., Jr., article, 544-553
Random versus systematic ecological sampling, test of, article, 499-512
Randomly dispersed individuals, some sampling characteristics of a population of, article, 741-757
Ranges of weeds, mass, climate as a factor influencing the, article, 308-321
Rat, Norway, physical environment of, 467
Rate of apparent photosynthesis of some broadleaf evergreens, article, 693-697
Rate of organic matter accumulation on the sedge mat zones of bogs in the Itasca State Park region of Minnesota, article, 81-101
Rausch, Robert, article, 584-604
Recession of eelgrass at Cape Ann, Massachusetts, note, 229-231
Redhorse, golden, home range of, 347
Redwoods, coast, and fog drip, note, 192-193
Reevaluation of plant communities within the pheasant range in the Nebraska sandhills, article, 771-777
Regulatory mechanisms in house-mouse populations: the effect of limited food supply on a confined population, article, 375-385
Report of the Three Kings Islands expedition, reviewed, 236
Reproduction in an animal population, affected by density, 488
Reproduction in house-mouse populations, 375
Reptiles, hibernation of, 74
Reptiles in Florida, 406
Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents, note, 225-229
Rhizopertha dominica, grain beetle, innate capacity for increase of, affected by food, temperature, and moisture, 698
Richards, P. W., reviewed, 808-810
Riegel, Andrew, co-author, article, 1-20
Roan Mountain conifer transplants to a grassy bald on, note, 614-617
Robocker, W. C., J. T. Curtis, and H. L. Ahlgren, note, 194-199
Rock bass, home range of, 347
Rocky Mountains, nutrient content of leaf litter of trees in the, article, 786-793
Role of lichens in soil formation and plant succession, note, 805-807
Role of plant ecology in biosystematics, note, 642-649
Rothschild, Miriam, and Teresa Clay, book notice, 240
Rudolph, Emanuel D., co-author, note, 805-807
Russell, Norman H., article, 366-374

S

Sagebrush, big, amounts of in plant communities near Tensleep, Wyoming, as affected by grazing treatment, note, 186-189
Salamander distribution in southern Appalachians, 436
Salamanders, hibernation studies of, 55
Salix spp., as food for moose, 102
Salton Sea, temperature regulation of young white pelicans at, 554
Sample plot size and shape in forest ecology, statistical efficiency of, article, 474-487
Sampling characteristics, some, of a population of randomly dispersed individuals, article, 741-757
Sampling, ecological, test of random versus systematic, article, 499-512
Sandhills, Nebraska, a reevaluation of plant communities within the pheasant range in the, article, 771-777
Saskatchewan, fescue grassland in, article, 386-405
Schein, Martin W., co-author, article, 467-473
Sea otter, *Enhydra lutris,* helminth parasites of, 584
Seasonal activity of green frog, 529
Seed plants, ecological life cycle of, note, 619-628
Seed treatments upon seedling emergence in seven browse species, comparative effect of, article, 778-785
Seedling emergence in seven browse species, comparative effect of seed treatments upon, article, 778-785
Seedlings, forest tree, effect of environmental conditions on survival and growth of, under field conditions in the Piedmont region of North Carolina, article, 667-688
Seedlings, native grass in Wisconsin, some factors affecting emergence and establishment of, note, 194-199
Shape, size and, the statistical efficiency of sample plot in forest ecology, article, 474-487
Sharp, Ward M., article, 771-777
Shelford, V. E., note, 422-426
Short grasses, effects of different intensities of clipping on in west-central Kansas, article, 1-20
Shrock, R. R., and W. H. Twenhofel, reviewed, 650-651
Size and shape in forest ecology, the statistical efficiency of sample plot, article, 474-487
Slobodkin, L. Basil, article, 513-519
Slobodkin, L. Basil, note, 430-434
Smith, F. E., co-author, note, 804-805

Smith, Frederick E., co-author, note, 223-224; 224-225
Smith, Osgood R., note, 636-637; 640-641
Snakes, hibernation of, 74
Social behavior in animals (Tinbergen), review, 810-811
Social single species populations, 430
Society for Experimental Biology, symposium, reviewed, 238-239
Sociology and ecology, fungus—II, survey of literature on, note, 211-222
Soil formation and plant succession, the role of lichens in, note, 805-807
Soil phosphates, the edaphic factor in plant ecology with a special note on, note, 426-428
Soil properties, surface, a comparison of under mesquite and perennial grass, article, 727-732
Some attempts toward experimental zoogeography, article, 657-666
Some feeding habits of moose in Yellowstone Park, article, 102-110
Some North American turtles and their epizoophytic algae, article, 733-740
Some sampling characteristics of a population of randomly dispersed individuals, article, 741-757
Some uses of vegetation maps, note, 629-636
Sperry, O. E., co-author, reviewed, 813-814
Spherical illumination as an ecological parameter, and an improved integrator, note, 416-421
"Spring lizard" industry: a factor in salamander distribution and genetics, note, 436-437
Srb, Adrian M, and Ray D. Owen, reviewed, 450-451
Stages in the evolution of plant species, reviewed, 233-235
Stanley, John, article, 21-28; 29-43
Statistical analysis applied to a vegetation type in New Zealand, article, 175-185
Statistical efficiency of sample plot size and shape in forest ecology, article, 474-487
Steppes becoming drier, are our? (Berg), note, 796-802
Storer, Tracy I., review, 449-450
Strecker, Robert L., and John T. Emlen, Jr., article, 375-385
Studies from the autotrephon. I. Some points in general operation and maintenance, article, 21-28
Studies from the autotrephon. II. The analysis of autotrephon data, article, 29-43
Studies on the helminth fauna of Alaska. XIII. Disease in the sea otter, with special reference to helminth parasites, article, 584-604
Study of hibernacula and hibernating associations of snakes and amphibians in Michigan, article, 74-80
Stullken, Donald E., and William A. Hiestand, article, 610-613
Substratum preferences of beetles, 657
Succession, plant, the role of lichens in soil formation and, note, 805-807
Sucker, home range of, 347
Sunfish, home range of, 347
Survey of literature on fungus sociology and ecology—II, note, 211-222
Survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina, effect of environmental conditions on, article, 667-688
Survival in house mouse populations, 375
Sutcliffe, W. H., Jr., note, 794-796
Synthesis of paleobiogeography (Termier), review, 811-813
Systematic ecological sampling, test of random versus, article, 499-512

T

Tabanids (flies), effect of weather on, 414
Temperature, affecting desert iguana, 265
Temperature, affecting hibernation of salamanders, 55
Temperature, affecting house mouse populations, 375
Temperature, affecting increase of grain beetles, 698
Temperature, affecting population density in an insect parasite, 322
Temperature control, influence of pelage pigmentation on, 610
Temperature regulation in young white pelicans, 554
Temporal variation in a small community of amphibians and reptiles, note, 406-408
Termier, H., and G. Termier, reviewed, 811-813
Territoriality in stream fishes, 347
Territoriality in the green frog, *Rana clamitans*, article, 165-174
Territoriality of desert iguana, 265
Test of random versus systematic ecological sampling, article, 499-512
Texas, east-central, quail in, 758
Theory, population, 430, 488, 513
Thermal maximum in southeastern Alaska, radiocarbon dating of, note, 637-640
Thermal preferences of beetles, 657
Thompson, Ernest F., review, 442-443
Thornthwaite climatic classification, palynology and the, note, 803-804
Three Kings Islands of New Zealand, review, 236
Tidal currents, effect on littoral invertebrates, 225
Tiffany, L. H., co-author, article, 733-740
Tinbergen, N., reviewed, 810-811
Transmission of flagellates in a lizard, 243
Transplants, conifer, to a grassy bald on Roan Mountain, note, 614-617

Trap for Cladocera, 223
Tribolium confusum, flour beetle, in autotrephon studies, 29
Trichomonas augusta, intestinal flagellate, in a lizard, 243
Tropical rain forest (Richards), review, 808-810
Turner, Harry J., Jr., note, 222-223
Turtles and epizoophytic algae, 733
Twenhofel, W. H., co-author, reviewed, 650-651
2, 4,-D, use of in the control of water hyacinth and alligator weed in the Mississippi delta, with certain ecological implications, note, 409-414

U

Urban rat population, physical environment of, 467
Use of 2, 4,-D in the control of water hyacinth and alligator weed in the Mississippi delta, with certain ecological implications, note, 409-414
Uses, some, of vegetation maps, note, 629-636
Utida, Syunro, article, 301-307
Utida, Syunro, co-author, article, 488-498

V

Vegetation maps, some uses of, note, 629-636
Vegetation type in New Zealand, statistical analysis applied to a, article, 175-185
Vegetation types in northwestern Alaska and comparisons with communities in other Arctic regions, article, 111-140
Vernberg, F. John, article, 55-62
Village sites, prehistoric Aleutian, ecology of, article, 246-264

W

Wagner, Kenneth A., co-author, article, 157-164
Warburton, Frederick E., note, 193-194
Water hyacinth and alligator weed in the Mississippi delta, use of 2, 4,-D in the control of, with certain ecological implications, note, 409-414
Water relations and chlorophyll content of forest herbs in southern Wisconsin, article, 544-553
Weather, effect on horsefly populations, 414
Weeds, mass ranges of, climate as a factor influencing the, article, 308-321
Wells, J. W., review, 650-651, 811-813
Went, F. W., co-author, article, 288-300
Where winter never comes. A study of man and nature in the tropics, reviewed, 447-449
Witchterman, Ralph, reviewed, 651-654
Wilson, Charles C., article, 693-697
Winter photosynthesis of *Picea excelsa,* article, 605-609
Wisconsin, native grass seedlings in, some factors affecting emergence and establishment of, note, 194-199
Wisconsin, southern, water relations and chlorophyll content of forest herbs in, article, 544-553
Woods Hole Oceanographic Institution, pub. reviewed, 442
Wyoming, amounts of big sagebrush in plant communities near Tensleep as affected by grazing treatment, note, 186-189

X

Xantusia vigilis, yucca night lizard, transmission of flagellates in, 243

Y

Yellowstone Park, feeding habits of moose in, 102

Z

Zoogeography, experimental, some attempts toward, 657
Zostera marina (eelgrass), recession of, 229